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Angela M. Johnson for the degree of Master of Science in Oceanography
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Title: An Investigation of the Distribution and Abundance of Ichthyoplankton and Juvenile Benthic Fishes in Relation to Nearshore Hypoxia within the Northern California Current System

Abstract approved:

Lorenzo Ciannelli

Nearshore hypoxia within the Northern California Current (NCC) system is a seasonal phenomenon caused by coastal upwelling and occurs mainly during late-summer and early fall. The effects of low oxygen levels on fish and invertebrate communities, particularly during early-life history stages, however, are poorly known for this area. I investigated the effects of hypoxia on the density, community structure, vertical and horizontal distribution of fish larvae and juveniles, as well as body condition of juveniles, along the central Oregon and Washington coasts during the summers of 2008 - 2011. During this sampling period, bottom dissolved oxygen (DO) values ranged from 0.49 to 9.85 ml l^{-1}, and the number of hypoxic (e.g., < 1.4 ml l^{-1}) stations sampled was low compared to 2002 and 2006 (only 54 sampling stations for the ichthyoplankton study out of 493, and only 12 stations out of 90 for the benthic juvenile study). From the ichthyoplankton study, I found that the overall density of fish larvae increased as bottom-DO values increased; however, the effect on individual species density was limited. Between 44.65 ^{o}N and 46.00 ^{o}N (~Florence, OR – Astoria, OR), fish

larvae altered their vertical distribution when bottom-DO was low by rising in shallower water layers.

From the benthic juvenile study, I found that English sole (*Parophrys vetulus*), butter sole (*Isopsetta isolepis*), speckled sanddab (*Citharichthys stigmaeus*) and Pacific sanddab (*Citharichthys sordidus*) dominated the catch with annual variation in abundances. Species composition, abundance and length had strong relationships with depth. Species abundance for English sole (< 75 mm), speckled sanddab (<100 mm) and Pacific sanddab also increased with increased bottom-DO. However, the body condition of butter sole (< 75 mm) and of large speckled sanddab (≥100 mm) increased with decreased bottom-DO.

Overall my research elucidates important patterns of larval and juvenile fish distribution within the NCC during summer. In both studies I have found a limited effect of DO on abundance, distribution and community assemblages. Variables other than DO, such as depth, season and location, dominated the explained variance of the intervening multivariate and univariate analysis. However, due to the paucity of samples during hypoxic events, continued monitoring of nearshore larval and juvenile species over varying hypoxic conditions is necessary for understanding the impact of hypoxia on these communities and subsequent adult populations.

An Investigation of the Distribution and Abundance of Ichthyoplankton and Juvenile Benthic Fishes in Relation to Nearshore Hypoxia within the Northern California Current System

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Angela M. Johnson

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Major Professor, representing Oceanography

Dean of the College of Earth, Ocean, and Atmospheric Sciences

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Angela M. Johnson, Author

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CHAPTER 1: LITERATURE REVIEW OF THE NORTHERN CALIFORNIA CURRENT LARVAL AND JUVENILE FISH COMMUNITIES AND PHYSICAL FACTORS IN THE SPRING-SUMMER SEASON

1.1 Thesis outline and overview

The northern California Current (NCC) has shown severe inner-shelf hypoxia (≤ 1.4 ml l^{-1}) and even water-column anoxia (0.0 ml l^{-1}) with the most recent anoxic event in 2006 (Chan et al. 2008). However, very few studies have investigated the impacts of hypoxia on the local fish communities within the NCC and even less on the early life stages of fishes. Therefore, I examined the effects of hypoxia on the density, community structure, vertical and horizontal distribution, and body condition of fish larvae and juveniles. In addition, I described the community structure of early life fishes for this region and changes to that structure during the upwelling season identified. I collected the data for the ichthyoplankton study from the central Oregon coast to the northern Washington coast during the summers of 2008, 2009, and 2010, and the data for the benthic study along the central Oregon coast off Moolack Beach from 2008-2011 during the summers only.

Before reviewing the results of this thesis, in Chapter 1 I will provide a general introduction highlighting the various aspects of this research project. Specifically, I will highlight the study location and ecological habitats, local area

upwelled-driven hypoxia, the larval and juvenile fish communities and distribution, and the research objectives.

1.2 Study location and habitat

The sampling stations for this project extended from Cape Perpetua, Oregon up to the northern tip of Washington, and therefore were all located within the northern California Current (NCC) system. The innershelf for this region changes in width from south to north along the Oregon coast and up along the Washington coast. Off Heceta Head, Oregon the shelf is very wide, but north of Heceta Head the shelf becomes much narrower until reaching the Columbia River. North of the Columbia River, along the Washington Coast, the shelf begins to widen, but not to the width off of Heceta Head. The benthic study (Chapter 3), however, was focused within the nearshore waters (< 100 m) of central Oregon, off Moolack Beach, Oregon. The nearshore benthic habitat off Moolack Beach is composed mostly of sandy bottoms with some rock outcrops (Romsos et al. 2007) and provide nursery and settlement locations for ecologically and commercially important species such as English sole (*Parophrys vetulus*), Dover sole (*Microstomus pacificus*), Pacific sanddab (*Citharichthys sordidus*), and rockfishes (*Sebastes* spp.), to name a few (Pearcy 1978, Krygier & Pearcy 1986).

The central Oregon coast has multiple economic uses. The site off of Moolack Beach, was recently selected for the location of the National Marine Renewable Energy Center Ocean Test Berths (Boehlert et al. 2007, Brekken et al. 2009). The location of the test berths is within my study area. Just south of the

sampling area is also the disposal site for the Yaquina Bay dredge. Both the influx of sand from the dredge and the addition of a bottom structure from the test berths, increase the need for further understanding the benthic ecosystem in this area.

1.3 Local area hypoxia

Upwelling systems located along eastern boundary currents experience annual coastal hypoxic events. Such events are caused by seasonal changes in wind patterns, which drive Ekman transport of surface water offshore. This movement of surface water offshore causes deep, nutrient-rich, oxygen-poor water to be upwelled onshore into the euphotic zone (Grantham et al. 2004, Barth et al. 2007). The Benguela Current in the eastern South Atlantic Ocean, the Humboldt Current in the eastern South Pacific Ocean, and the California Current in the eastern North Pacific Ocean are examples of eastern boundary current upwelling systems. These systems support highly productive fisheries, particularly anchovy and sardine (Pauly & Christensen 1995, Ekau & Verheye 2005), due to the high primary productions resulted from nutrient loads brought to the coast with the upwelling currents (Falkowski et al. 2011). Along with the input of nutrients, low levels of oxygen are brought to the nearshore system from the offshore oxygen minimum zones (OMZ). Respiration from microorganisms within the water column further decreases the oxygen content of the upwelled waters. The onset and temporal extent of stratification within the water column is also essential to get hypoxic bottom waters.

The NCC along the western United States (Washington, Oregon and Northern California) has shown inner-shelf hypoxia (1.43 ml l^{-1}), severe inner-shelf hypoxia ($\leq$ 0.5 ml l^{-1}) and even water-column anoxia (Chan et al. 2008). These hypoxic regions can cover a large portion of the shelf along the Oregon and Washington coasts by late summer. In central Oregon, inner-shelf hypoxia (< 80 m) has been documented annually since 2000 (Grantham et al. 2004, Chan et al. 2008). Hypoxic events along the shelf tend to first occur near the bottom but can extend up through the water column to within 10-15 m of the surface (Chan et al. 2008).

Barth et al. (2007) noted that the NCC experiences more variable alongshore wind patterns than the southern California Current (SCC) due to eastward-traveling Gulf of Alaska low-pressure systems, which create periods of relaxation in between periods of strong favorable upwelling. These relaxation events prevent oxygen-poor bottom water from mixing with oxygen-rich surface water, therefore increasing the stratification of low dissolved oxygen (DO) within the water column. The relaxation of favorable upwelling winds can also minimize the offshore transport of surface water and impact recruitment of larval marine organisms within the water column (Shanks et al. 2000, Miller & Shanks 2004, Shanks et al. 2005, Barth et al. 2007). Falkowski et al. (2011) suggests that global climate change could have an indirect effect on the extent and spatial distribution of nearshore hypoxic events within the NCC. Wind patterns have started to change as the earth warms and sea level rises. Stronger and more intense wind

forcing along the NCC during the summer could cause more intense and extensive upwelling, which in turn could cause expansive and temporarily extensive hypoxic events. Keeling et al. (2010) and Stramma et al. (2010) are already measuring decreases in DO within the OMZ in the North and the tropical Pacific, and the tropical Atlantic and Indian gyres due to global warming.

Low DO can alter the biogeochemical cycling of elements, distribution of marine species, and impact the economic status of many coastal communities (Helly & Levin 2004, Rabalais et al. 2010, Zhang et al. 2010). Organisms rely on oxygen to perform many physiological processes (Wang et al. 2009). Therefore, low DO may cause organisms to change their behavior and physiology in order to increase their survival during periods of hypoxia (Wu 2002). These hypoxia driven changes in behavior, when compared with behaviors during normoxic conditions, have been shown to increase mortality, starvation, and physiological stress and reduce growth rates and available habitat space for certain organisms (Chabot & Dutil 1999, Tallqvist et al. 1999, Breitburg 2002, Gray et al. 2002, Rabalais et al. 2002, Wu 2002, Bell & Eggleston 2005). The level of DO that begins to cause changes in various organisms differs among taxa (Vaquer-Sunyer & Duarte, 2008). Of the four groups Vaquer-Sunery & Duarte (2008) investigated (crustaceans, fishes, bivalves and gastropods), gastropods had the lowest median lethal oxygen threshold (<1.0 mg O^2 l^{-1}), while crustaceans (several species of decapods and amphipods) showed significantly higher median lethal DO

thresholds than fishes, bivalves and gastropods. The mean lethal concentration for all organisms in their study was 2.05 mg O^2 l^{-1} (2.0 ml $^{-1}$).

Hypoxia can vary vertically and horizontally throughout the water column, with the most intense hypoxic waters occurring at the bottom boundary layer (BBL). Many studies have focused therefore on the tolerance of benthic organisms to low DO (Dauer & Ranasinghe 2002, Diaz & Rosenberg 1995, Miller et al. 2002, Alteri 2008, Vaquer-Sunyer & Duarte 2008, Zhang et al. 2010) but few studies have investigated the effects of low DO on pelagic fish, particularly during early life stages and in upwelling-driven systems. Benthic organisms are less sensitive to low DO than pelagic organisms with bivalves and polychaetes having higher tolerances than crustaceans and fish due to the ability of bivalves and polychaetes to alter their behavior and physiology (Diaz & Rosenberg 1995, Vaquer-Sunyer & Duarte 2008, Zhang et al. 2010). Miller et al. (2002) observed 50 % mortality for certain early life benthic (e.g. juvenile bivalve *Spisula solidissima*) and pelagic (e.g. larval and juvenile Osteichthyes, and larval, post-larval and juvenile crustaceans) species when DO was between 0.4 – 1.9 mg l^{-1} (0.4 – 1.9 ml l^{-1}) with pelagic larvae generally more sensitive than benthic larvae. Ekau & Verheye (2005) found that larval *Sardinops sagax* (sardines), *Trachurus trachurus capensis* (horse mackerel), and larval mesopelagic fish densities were closely related with DO concentrations, with higher catch densities in well-oxygenated waters (> 4.0 ml l^{-1}).

Studies have also shown that pelagic fish alter their vertical and horizontal distributions to remain above or outside the hypoxic boundary layer when bottom-DO values are more severely hypoxic, reducing the available habitat for these species (Keister et. al. 2000, Taylor & Rand 2003, Klumb et al. 2004, Bell & Eggleston 2005, Taylor et al. 2007, Parker-Setter & Horne 2008, Ludsin et al. 2009 Vanderploeg et al. 2009, Zhang et al. 2009). Mesozooplankton, on the other hand, have been shown to take "refuge" within the hypoxic boundary layer creating a separation of predator and prey (Taylor & Rand 2003, Klumb et al. 2004, Taylor et al. 2007, Parker-Setter & Horne 2008, Ludsin et al. 2009 Vanderploeg et al. 2009, Zhang et al. 2009). Keister et al. (2000) observed that ctenophores, a mesoplankton and ichthyoplankton predator, were abundant when DO was very low (1.3 mg O^2 l^{-1}). Vertical migration patterns of pelagic fish have also been interrupted during severe hypoxic events (Taylor et al. 2007, Ludsin et al. 2009, Zhang et al. 2009) creating changes in food web dynamics. Collectively, these studies demonstrate that pelagic species can also be negatively affected by hypoxia, particularly during their early life stages.

1.4 Larval and juvenile fish community

The nearshore (< 80 m depth) larval fish community along coastal Oregon and Washington is highly diverse with over 70 taxa represented (Richardson & Pearcy 1977, Brodeur et al. 2008). *Engraulis mordax* (Northern anchovy), *Sebastes* spp. (rockfishes), *Microgadus proximus* (Pacific tomcod), *Artedius* spp. (sculpins), *Stenobrachius leucopsarus* (Northern lanternfish), and *Lyopsetta exilis*

(slender sole) have been identified as dominant larval taxa collected during the spring and summer along the Oregon and Washington Coasts (Richardson & Pearcy 1977, Auth & Brodeur 2006, Brodeur et al. 2008). Distinct larval fish assemblages of the NCC have been characterized for coastal (~ < 90 m depth) and offshore habitats (> 90 m depth) (Richardson & Pearcy 1977, Auth & Brodeur 2006, Auth 2011). Both the coastal and offshore assemblages peak in abundance between February and July (Richardson & Pearcy 1977). Coastal assemblages have been dominated by Osmeridae (smelts), *Parophrys vetulus* (English sole), *Isopsetta isolepis* (butter sole), and Pacific tomcod, while offshore assemblages have been dominated by rockfishes, *Stenobrachius leucopsarus* (Northern lanternfish), *Tarletonbeania crenularis* (blue lanternfish), slender sole, and Northern anchovy (Richardson & Pearcy 1977, Auth & Brodeur 2006, Auth 2011).

The nearshore benthic fish community is biologically rich and dominated by Pacific sanddab, sand sole (*Psettichthys melanostictus*), speckled sanddab (*Citharichthys stigmaeus*) and Pacific tomcod (Pearcy 1978, Wakefield 1984). Many of the species in this region vary in life history strategies and feeding habits to create a very complex and dynamic ecosystem (Kravitz & Pearcy 1976, Wakefield 1984). Benthic assemblages have been characterized by sediment type and depth (Pearcy 1978, Toole et al. 2011). Toole et al. (2011) concluded that flatfishes dominated the mid-shelf, while gadids, scorpaenids, osmerids, and zoarcids dominated the outer-shelf and slope. However, no studies have investigated the effects of dissolved oxygen on the distribution of species in

nearshore benthic communities along the central Oregon coast. Because fish early life stages are less tolerant to low DO than their adult counterparts (Keister et al. 2000, Miller et al. 2002, Zhang et al. 2010), they need special considerations when studying species response to hypoxia. This research need is particularly relevant for eastern boundary systems, characterized by both, coastal hypoxic events, and an abundant fish biomass.

1.5 Research Objectives

The overarching goal of this study is to fill in the missing knowledge of the effects hypoxia has on early life stages of fishes within the NCC. My objectives are to investigate the effects of hypoxia 1) on the density, community structure, vertical and horizontal distribution of ichthyoplankton (Chapter 2), and 2) on the abundance, community structure, horizontal and body condition of juvenile benthic fishes (Chapter 3). In addition, I will describe the community structure of benthic and pelagic early life history stages of fishes for this region and identify any changes during the upwelling season due to other abiotic factors such as bottom temperature, depth, season and year. Collectively, these results will help us to characterize the effect of DO on fish early life stages in upwelling driven systems and provide baseline information to assess the potential impact of coastal developments (e.g., wave energy farms, dumping of dredge material, etc) which, can be integrated in ongoing planning efforts for the usage of Oregon coastal waters (coastal marine spatial planning initiatives).

CHAPTER 2: Ichthyoplankton distribution and abundance in relation to nearshore dissolved oxygen levels within the Northern California Current System

2.1 Abstract

Nearshore hypoxia along the coast of Oregon and Washington is a seasonal phenomenon that has generated concern among scientists studying this temperate upwelling ecosystem. These waters are affected by coastal upwelling-induced hypoxia mainly during late summer and fall, but effects of low oxygen levels on fish and invertebrate communities, particularly during early-life history stages recruiting and settling during the summer and fall, are poorly known. I investigated the effects of hypoxia on the species composition, density, vertical, and horizontal distribution of fish larvae along the Oregon and Washington coasts during the summers of 2008, 2009, and 2010. Bottom dissolved oxygen (DO) values ranged from 0.49 - 4.79 ml l^{-1} over all sample years, but the overall water column DO values were only moderately hypoxic during the three years of sampling compared to previous extreme years (e.g., 2002 and 2006). DO was not a dominant environmental parameter driving the species composition of this study. Instead salinity and Julian Day had the strongest correlations with species composition. I did find, that the overall density of fish larvae increased as bottom-DO values increased; however, the effect on individual species density was limited. Slender sole (*Lyopsetta exilis*) and sand sole (*Psettichthys melanostictus*) were the only species to have significant relationships with DO and both showed

negative relationships. Finally, in certain locations within my sampling region, fish larvae altered their vertical distribution when bottom-DO was low by rising into shallower water layers. The sampling of severe hypoxic events was limited and my results indicate that larval fish spatial distribution was not greatly affected within the range of observed values. More continuous sampling, over a greater range of DO values, is necessary to better characterize the effect of hypoxia on the ichthyoplankton community of the Oregon and Washington coast.

2.2 Introduction

Increasing reports of hypoxic events in coastal and estuarine waters since the late 1990s, have garnered the interest of both the scientific and fishing communities. Scientific investigators are trying to understand the driving mechanisms of nearshore hypoxic events and their consequences for local ecosystems (Diaz & Rosenberg 2008, Vaquer-Sunyer & Duarte 2008, Rabalais et al. 2010). Low dissolved oxygen (DO) can alter the biogeochemical cycling of elements and distribution of marine species, thus potentially impacting the economic status of many coastal communities (Helly & Levin 2004, Rabalais et al. 2010, Zhang et al. 2010). Coastal hypoxia is caused by increased nutrient enrichment and higher respiration in nearshore areas. The mechanisms for nutrient enrichment can vary and are linked to either human activities, as seen in the Gulf of Mexico, Chesapeake Bay, and the Adriatic Sea (Diaz 2001, Breitburg et al. 2003, Rabalais et al. 2010), or the surfacing of nutrient-rich, oxygen-poor, deep water from the oxygen minimum zone (OMZ) by upwelling favorable winds, as

seen within eastern boundary current ecosystems (Grantham et al. 2004, Ekau & Verheye 2005, Barth et al. 2007, Bograd et al. 2008, Rabalais et al. 2010, Zhang et al. 2010). The increased inputs of nutrients to surface waters, in turn, increase primary production at the surface. Although the elevated primary production increases the amount of food available for higher trophic level organisms, production often exceeds consumption resulting in the settlement and accumulation of organic matter and an increase in microbial respiration, further reducing oxygen concentrations in bottom waters (Breitburg 2002, Diaz & Rosenberg 2008, Breitberg et al. 2009). Upwelling systems located along eastern boundary currents experience annual coastal hypoxic events caused by seasonal changes in wind patterns (Grantham et al. 2004, Barth et al. 2007). The Benguela Current in the eastern South Atlantic Ocean, the Humboldt Current in the eastern South Pacific Ocean, and the California Current in the eastern North Pacific Ocean are examples of eastern boundary current upwelling systems. These systems have been shown to support highly productive fisheries, particularly for anchovies and sardines (Pauly & Christensen 1995, Ekau & Verheye 2005).

The northern California Current (NCC) along the western United States (Washington, Oregon, and northern California coasts) has shown inner-shelf hypoxia ($\leq$1.43 ml l^{-1}), severe inner-shelf hypoxia ($\leq$ 0.5 ml l^{-1}) and even water-column anoxia in recent years (Chan et al. 2008, Connolly et al. 2010, Pierce et al. 2012). These hypoxic regions can cover a large portion of the shelf along the Oregon and Washington coasts by late summer (Grantham et al. 2004, Connolly et

al. 2010). Inner-shelf (< 50 m) hypoxia has been documented annually since 2000, along the central Oregon coast (Grantham et al. 2004, Chan et al. 2008, Pierce et al. 2012). Hypoxic events along the shelf tend to first occur near the bottom but can extend up through the water column to within 10 - 15 m of the surface (Chan et al. 2008).

Hypoxia can vary vertically and horizontally throughout the water column, with the most intense hypoxic waters occurring at the bottom boundary layer (BBL). Therefore, many studies have focused on the tolerance of benthic organisms to low DO (Diaz & Rosenberg 1995, Miller et al. 2002, Altieri 2008, Vaquer-Sunyer & Duarte 2008, Zhang et al. 2010), but relatively few studies have investigated the effects of low DO on pelagic fish, particularly during early-life stages and in upwelling-driven systems. Organisms rely on oxygen to perform many physiological processes. Low DO may cause organisms to change their behavior or undergo physiological adaptations in order to increase their survival during hypoxic conditions (Wu 2002). However, these hypoxia-driven changes in behavior, if protracted over time, have also been shown to increase mortality, starvation, and physiological stress and reduce growth rates and available habitat space for certain organisms compared with behaviors during normoxic conditions (Chabot & Dutil 1999, Tallqvist et al. 1999, Breitburg 2002, Gray et al. 2002, Rabalais et al. 2002, Wu 2002, Bell & Eggleston 2005, Herbert et al. 2010, McClatchie et al. 2010). Vaquer-Sunyer & Duarte (2008) observed that the levels of DO that begin to cause changes in various organisms differ among taxa.

Previous studies have shown that pelagic fish alter their vertical and horizontal distributions to remain above or outside the hypoxic boundary layer when bottom-DO values are more severely hypoxic, reducing the available habitat for these species (Keister et. al. 2000, Taylor & Rand 2003, Klumb et al. 2004, Bell & Eggleston 2005, Prince & Goodyear 2006, Taylor et al. 2007, Parker-Stetter & Horne 2008, Ludsin et al. 2009 Vanderploeg et al. 2009, Zhang et al. 2009, Herbert et al. 2010). Vertical migration patterns of pelagic fish have also been interrupted during severe hypoxic events (Taylor et al. 2007, Ludsin et al. 2009, Zhang et al. 2009), creating changes in predator/prey spatial overlap. Fish early-life stages appear to be less tolerant to low DO than their adult conspecifics (Keister et al. 2000, Miller et al. 2002, Zhang et al. 2010). Thus, further investigations into the effects of low DO on pelagic fish early-life stages are needed, in order to understand the development and survival of larval fishes in areas that experience hypoxia. This research need is particularly relevant for eastern boundary current systems, characterized by both coastal hypoxic events and abundant fish biomass.

Larval fish distributions during upwelling seasons along the Oregon and Washington coasts have been analyzed in relation to shelf dynamics, depth, temperature, and salinity (Auth & Brodeur 2006, Auth et al. 2007, Auth 2008, Parnel et al. 2008, Brodeur et al. 2008, Auth 2011), but few studies have investigated the relationship of larval fish to DO in this region (Auth 2011). Any changes to larval fish community dynamics can alter the success of local adult fish

stocks in an ecosystem (Sherman et al. 1983, Houde 2008). The nearshore larval fish community along the central Oregon coast is relatively diverse with over 70 taxa represented (Richardson & Pearcy 1977, Brodeur et al. 2008). The dominant taxa of coastal larval fish collected during spring and summer along the nearshore Oregon and Washington coasts are: *Engraulis mordax* (Northern anchovy), *Sebastes* spp. (rockfishes), and members of the families Osmeridae, Pleuronectidae, Hexagrammidae, and Cottidae (Richardson & Pearcy 1977, Doyle et al. 1993, Auth & Brodeur 2006, Brodeur et al. 2008).

The aim of this study was to investigate the effects of hypoxia on the density, composition, horizontal and vertical distribution of fish larvae along the Oregon and Washington coasts during three summers: 2008, 2009, and 2010. I focused this study on the shelf system (< 100-m depth) concentrating on coastal hypoxic events, which are seasonal phenomena with peak intensity during summer (Barth et al. 2007, Rabalais et. al. 2010). I hypothesized that 1) hypoxia would have a negative effect on the local density of fish larvae, which would ultimately result in changes in horizontal distribution patterns and community structure, and 2) the proportion of the water column inhabited by fish larvae will decrease during intense hypoxic events (Taylor & Rand 2003, Prince & Goodyear 2006, Taylor et al. 2007, Ludsin et al. 2009, Vanderploeg et al. 2009, Zhang et al. 2009). Thus, as a corollary of these two hypotheses, I predicted that densities of larval fish would be positively correlated with DO concentrations.

2.3 Methods

2.3.1 Sampling sites and gear

I sampled during 25 different cruises, some single day and some multiple days, between late May and early September from 2008-2010. Cruises occurred on the OSU R/V Elakha, OSU R/V Wecoma and the NOAA R/V Miller Freeman. The sampling sites occurred along the continental shelf between Yachats, Oregon (~ 44^{o}N) and Neah Bay, Washington (48.5^{o}N) (Fig. 1). Depth of sampling sites ranged from 20 m to 400 m, but most of the sampling (95%) occurred at depths ≤ 100 m with an overall average sampling depth of ~ 80 m. I collected the samples using the Hydro-Bios Multi Plankton Sampler MultiNet Type *Midi* system (Hydro-Bios, Kiel, Germany, www.hydrobios.de) with a mouth area of 0.5 m^{2}. This system has five 300-µm mesh nets attached to the main unit that are opened and closed via a motor unit either preprogrammed based on depth prior to deployment, or signaled by a live-wire connection to a deck command unit located on the research vessel while sampling. The MultiNet is equipped with an integrated pressure sensor, which allows for continuous monitoring of operating depth and two electronic flow meters that allow for monitoring of tow speed and net orientation in the water column, as well as determination of volume of water filtered per sample. Mounted on top of the net frame was a CTD-DO unit that contained conductivity, pressure, temperature, and DO sensors. At each site, I opened the first net when the MultiNet was deployed to < 10 m from the bottom. The remaining nets were opened every 10 - 20 m depending on the depth of the sampling site.

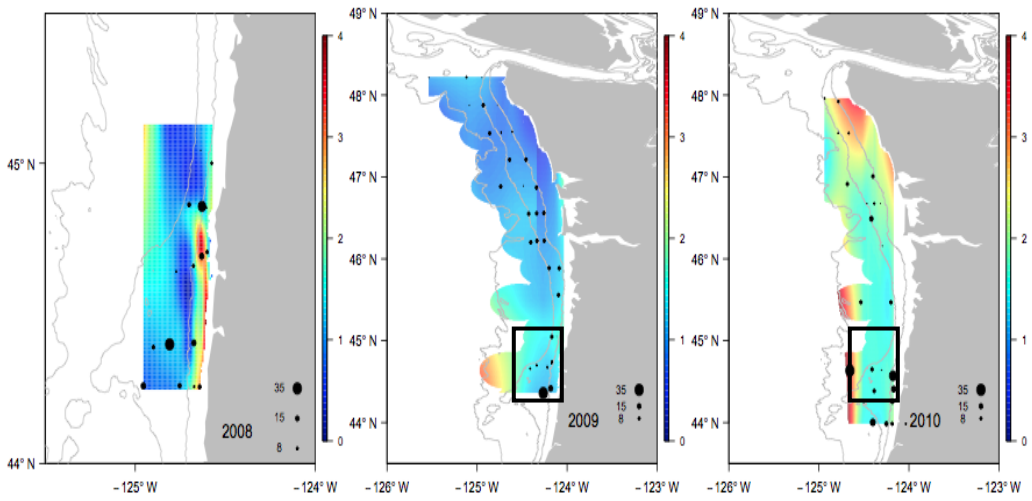

Figure 1. Study area for all sample years 2008 – 2010, between late May and early September. The color scale represents the lowest bottom dissolved oxygen (ml l^{-1}) for the sample region, while the black filled circles represent the average standardized fish count (no. m^{-3} x 100) per location. The solid black square in the 2009 and 2010 maps represent the 2008 sample area.

For deeper sites, nets remained open longer, sampling a greater vertical distance (e.g., at 150-m bottom depth nets were opened every 20 m, whereas at 80-m bottom depth, nets were opened every 10 - 15 m). The depths at which nets were opened-closed were referenced from the bottom, rather than the surface, since gradients of DO content are sharper closer to the bottom. Throughout this paper, the maximum depth at which each net, during one tow, was opened will be referred to, as the 'sample depth,' while the depth at that station will be referred to as the 'bottom depth'. The MultiNet was towed obliquely at a ship speed of 1 - 2 m s^{-1} and a wire-retrieval speed of 10 m min^{-1} with an average net volume filtered of 40 m^3. At the end of each tow, samples were removed from the five cod ends and stored in a 10 % formaldehyde/seawater mixture. In the lab, each sample was measured for biovolume, biomass, and larval fish were counted and identified to the lowest possible taxon. At each sampling location, I also made an additional deployment of a CTD (Sea-Bird Electronics Model 25, Bellevue, WA, USA) equipped with a flow-through DO sensor throughout the water column.

2.4 Analytical methods

2.4.1 Multivariate, Diversity and Evenness Analyses

The effects of environmental factors on larval fish composition were examined with a non-metric multidimensional scaling (NMS) analysis, a non-parametric ordination method (Kruskal 1964). I used Sorensen (Bray-Curtis) distance measure with random starting positions and 50 runs with real data. The species matrix contained standardized abundance measures of fish m^{-3} for taxa that

occurred in more than 3.0% of the samples. The environmental matrix contained five continuous variables (Julian day, maximum depth of each net, lowest salinity of each net, lowest temperature of each net, and lowest DO of each net) and the six categorical variables (season, year, time of day, latitude, DO, and sample depth). I divided the variable season into two categories: early (samples that occurred before July 15th) and late (samples that occurred on or after July 15th); the variable year into three categories: 2008, 2009, and 2010; the variable time of day into two categories: day (between sunrise and sunset) and night (between sunset and sunrise); the variable latitude into three categories: north (46.00^{o}N – 48.00^{o}N), central (44.65^{o}N – 46.00^{o}N) and south (44.00^{o}N - 44.65^{o}N); the variable DO into five categories: 1 (0.00 - 1.49 ml l^{-1}), 2 (1.50 - 1.99 ml l^{-1}), 3 (2.00 - 2.99 ml l^{-1}), 4 (3.00 - 3.99 ml l^{-1}), and 5 (≥ 4.00 ml l^{-1}); and the variable sample depth into five categories: 1 (0.0 - 24.9 m), 2 (25.0 - 49.9 m), 3 (50.0 - 74.9 m), 4 (75.0 - 99.9 m), and 5 (≥ 100.0 m). I established the latitude, DO and sample depth categories based on previous studies (Richardson & Pearcy 1977, Doyle et al. 1993, Ekau & Verheye 2005, Auth & Brodeur 2006, Auth 2008, Parnel et al. 2008, Vaquer-Sunyer & Duarte 2008). No samples were collected at dusk or dawn during this study.

I conducted a multi-response permutation procedure (MRPP) using the Sorensen (Bray-Curtis) distance measure to investigate whether there were significant differences between groups within each categorical variable. For each categorical variable, an A-statistic and p-value are reported from the MRPP

analysis. The A-statistic refers to the chance-corrected, within-group agreement, so that when A = 1 there is homogeneity within groups and when A = 0 there is heterogeneity within groups (McCune & Grace 2002). The p-value from the MRPP analysis indicates how likely an observed difference between groups is due to chance (McCune & Grace 2002). Where significant differences occurred, an indicator species analysis (ISA) was used to determine if any of the species used in the ordination analysis were significant indicators for those groups (Mielke & Berry 2001). During the ISA, 4999 permutations were conducted in the Monte Carlo test. Taxa were considered significant indicators at $p < 0.05$, with a 95% confidence interval. I conducted these statistical analyses using PC-Ord v.6 (McCune & Grace 2002).

Finally, I measured diversity and evenness of the larval fish community for taxa that occurred in more than 3.0% of the samples across six categorical variables: season, year, sample depth (m), time of day, latitude, and DO (ml l^{-1}), as previously defined in the multivariate analyses. Diversity and evenness were measured using the Shannon-Wiener Index (H') and Pielou's Index (J') respectively. Higher H' values indicate the greatest diversity (Whittaker 1972). Evenness (J') values ranged from 0 to1, with larger values indicating that all taxa are present in the same relative concentrations (Pielou 1969).

2.4.2 Horizontal distribution analysis & Individual responses to DO

Larval fish abundances, excluding zero catch data, were standardized by volume (m^3) then summed over all five nets at each site and correlated to bottom

depth to determine if horizontal distribution of fish larvae varied with changes in DO. A Generalized Additive Model (GAM, Wood 2008) in the statistical package *R* v. 64 (The R Foundation for Statistical Computing, http://www.r-project.org) was used for this comparison. The GAM used a Gaussian family model and identity link function. The response variable, standardized larval fish abundance (F_i), was natural log-transformed to satisfy the assumption of normality. Season (M_i), time of day (D_i), latitude (L_i), bottom depth (Z_{bi}), bottom DO (BDO_i), sea-surface salinity (S_i) and sea-surface temperature (T_i) were included as covariates in the model. The following variables were included as factors: latitude, season, time of day, and bottom depth. Latitude refers to the sample region: north ($46.00^oN – 48.00^oN$), central ($44.65^oN – 46.00^oN$), or south ($44.00^oN - 44.65^oN$). I divided the factor latitude into three regions based on conclusions found in previous studies of larval fish abundance and recruitment and shelf dynamics (Richardson & Pearcy 1977, Doyle et al. 1993, Parnel et al. 2008, Auth 2008). I divided the factor season into early (late May – mid July) and late (mid July – September), and the factor time of day into day (sunrise – sunset) and night (sunset – sunrise). Sampling did not occur at dusk or dawn during this study. The factor bottom depth was divided into four categories (1 = < 50 m, 2 = 51 - 75 m, 3 = 76 - 100 m, 4 = > 100 m). The following GAM was fitted where 's' refers to a smoothing function:

$$\log(F_i + 0.1) \sim s(\log(BDO_i)) + s(S_i) + s(T_i) + M_i + L_i + D_i + Z_{bi}$$

Individual species responses to changes in DO were measured for the twelve most

abundant taxa using linear regression analysis with the statistical package *R* v. 2.10.1.

2.4.3 Vertical distribution analysis

The effect of hypoxia on the vertical distribution of fish larvae abundance was investigated by first calculating the standardized weighted average depth of fish m^{-3} caught for each tow, and comparing this across different values of bottom DO using an ANCOVA. The analysis was applied to tows with a positive fish catch only (e.g., at least 1 net within a tow had at least 1 larval fish). The equation used for calculating the standardized weighted average (Z_{fi}) depth is:

$$\Sigma (F_i * d_i)/ \Sigma (F_i) = Z_{di}$$

$$1 - (Z_{di}/ Z_{bi}) = Z_{fi}$$

where F_i equals each standardized fish count for each net (1 - 5) at each site, d_i equals the max depth, or sample depth, for each net (1 - 5) at each site. Bottom depth (Z_{bi}) is the bottom depth for that tow. First, I calculated the average depth of fish occurrence for each tow (Z_{di}) by summing the standardized fish abundance (F_i) divided by sample depth (d_i) the dividing by the sum of standardized fish abundance (F_i). I then calculated the weighted average depth of fish larvae (Z_{fi}) by taking the ratio of (Z_{di}/Z_{bi}) and subtracting from 1 in order to graph the results so that '1' referred to the surface while '0' referred to the bottom. The weighted average depth was logit-transformed so that it would not be constrained from 0 - 1 in the statistical analysis. The following ANCOVA model was fitted using the statistical package *R* (v. 2.10.1):

$$\text{logit}(Z_{fi}) \sim BDO_i + L_i + M_i + D_i$$

The factors latitude (L_i), season (M_i) and time of day (D_i) are the same as described in the previous GAM analysis. Finally, I conducted a Tukey multiple comparison test with a 95% family-wise confidence level for any factor with a significant relationship indicated by the ANCOVA. In addition to the analysis of vertical distribution of the entire larval community, I also performed an analysis of vertical distribution for each of the top twelve most abundant taxa, using positive catches only. In this case, however, I conducted simple linear regressions as opposed to an ANCOVA to compare vertical distributions to DO (ml l^{-1}).

Because fish larvae can change their vertical distribution in relation to both absolute values of DO and/or the thickness of the bottom hypoxic layer, the I also compared the weighted average depth (Z_{fi}) of ichthyoplankton to the depth of the hypoxic layer (HL_i). The following factors were again considered in this analysis: latitude (L_i), season (M_i), and time of day (D_i). I again used an ANCOVA followed by a Tukey multiple comparison test with a 95% family-wise confidence level for any factor with a significant relationship indicated by the ANCOVA. I determined the thickness of the hypoxic layer as the distance between the bottom and the depth at which DO = 2.0 ml l^{-1}, therefore I only used tows with positive fish catches and bottom DO values of 2.0 ml l^{-1} or less in this analysis. The weighted average (Z_{fi}) was logit-transformed and standardized to the total depth as in the previous analysis, and I estimated the effects of the hypoxic layer, latitude,

season and time of day on the fish weighed average depth as follows:

$$\text{logit}(Z_{fi}) \sim HL_1 + L_i + S_i + T_i$$

2.5 Results

Overall, 493 samples were collected during the upwelling season between late May and early September in the three years of sampling (Table 1). Fish larvae representing 23 taxa were found in the 197 samples that contained fish larvae. The bottom DO range, total fish count, and taxonomic standardized abundance (fish m^{-3}) varied among years (Table 2). Each year differed from the next in hypoxia occurrence and intensity, with 2010 having the weakest hypoxia event. Together, rockfishes (*Sebastes* spp.) and slender sole (*Lyopsetta exilis*) made up more than 25% of the total catch for all three years combined. The DO range of fish catch also varied among the taxa (Table 2). Rockfishes, slipskin snailfish (*Liparis fucensis*), butter sole (*Isopsetta isolepis*), and slender sole were the only taxa caught when DO was < 1.4 ml l^{-1} (Table 2).

2.5.1 Multivariate, Diversity and Evenness Analyses

The best NMS model resulted in a three dimensional solution that explained 62.3% of the variance. Of the three axes, axis 2 explained the most variance (23.4%), while axis 1 and axis 3 explained 19.8% and 19.2%, respectively. Max net depth was most correlated with axis 2 (r = -0.208) while dissolved oxygen was most correlated with axis 1 (r = -0.192) and salinity most

Table 1. Summary of sample dates, number of samples collected, percent of samples with fish, total number of fish, total number of taxa, and dissolved oxygen ranges for each sample year 2008, 2009 and 2010 and the totals over all 3-sample years. Samples refer to each net fished.

	Sample dates	Samples collected	Samples with fish	Total no. of Fish m^{-3}	Total no. of taxa	Bottom-DO Range (ml l^{-1})
2008	May 24-Sept. 1	155	35%	0.015	18	0.71 - 4.79
2009	June 12-Aug. 22	182	19%	0.029	10	0.49 - 1.56
2010	June 16-20 Aug. 4-9	156	68%	0.041	17	1.22 - 3.67
Total		493	40%	0.027	23	

Table 2. Mean standardized abundance ((fish m^{-3})*100) and standard deviation in () for each taxon by sample year: 2008 - 2010. Included is the range of dissolved oxygen (ml l^{-1}) values in which each taxon were collected during the reported sample seasons. * = top twelve dominant taxa over all three years used in further analyses.

Family	Taxon	Common name	2008	2009	2010	DO range
Engraulidae	*Engraulis mordax**	Northern anchovy	0.115 (0.012)	-	0.055 (0.005)	1.8-5.8
Osmeridae	Unidentified osmeridae	Smelts	0.019 (0.003)	-	-	1.8-3.7
Myctophidae	*Stenobrachius leucopsarus**	Northern lanternfish	0.308 (0.024)	-	0.277 (0.01)	2.1-5.7
Scorpaenidae	*Sebastes* spp. *	Rockfishes	0.844 (0.035)	0.073 (0.005)	0.999 (0.044)	1.2-6.1
Cottidae	*Artedius fenestralis* *	Padded sculpin	0.093 (0.005)	0.030 (0.004)	0.656 (0.040)	1.8-3.8
	Artedius lateralis	Smoothhead sculpin	0.045 (0.005)	0.009 (0.001)	0.015 (0.002)	1.8-2.0
	Artedius harringtoni *	Scalyhead sculpin	0.011 (0.002)	0.038 (0.003)	0.147 (0.009)	2.4-5.5
	Artedius spp.*	Sculpins	-	0.032 (0.003)	0.105 (0.007)	2.0-6.2
	Radulinus asprellus	Slim sculpin	0.097 (0.010)	0.006 (0.001)	0.021 (0.003)	1.5-1.9
	Chitonotus pugetensis	Roughback sculpin	0.036 (0.004)	-	-	2.3
	Leptocottus armatus *	Pacific staghorn sculpin	0.134 (0.010)	-	0.102 (0.007)	1.9-4.7
Liparidae	*Liparis fucensis**	Slipskin snailfish	0.095 (0.005)	0.050 (0.003)	0.168 (0.008)	1.3-5.1
	Liparis gibbus	Variegated snailfish	0.035 (0.004)	-	-	1.8-4.7
	Liparis mucosus	Slimy snailfish	0.027 (0.003)	-	-	2.5-3.7
	Liparis spp.	Snailfishes	0.015 (0.002)	-	0.023 (0.003)	2.4
Stichaeidae	*Poroclinus rothrocki*	Whitebarred prickleback	-	-	0.113 (0.014)	1.8
	Anoplarchus purpurescens	High cockscomb	0.009 (0.001)	-	-	1.7
Paralichthyidae	*Citharichthys sordidus* or *stigmaeus*	Pacific or Speckled sanddab	0.007 (0.001)	-	-	3.2
Pleuronectidae	Unidentified pleuronectidae *	Right-eye flatfish	0.032 (0.004)	0.174 (0.016)	0.291 (0.017)	1.5-5.9
	*Isopsetta isolepis**	Butter sole	0.059 (0.006)	0.017 (0.002)	0.030 (0.003)	1.2-2.6
	*Lyopsetta exilis**	Slender sole	0.088 (0.010)	0.873 (0.051)	1.328 (0.041)	1.0-5.7
	*Psettichthys melanostictus**	Sand sole	-	0.064 (0.007)	0.204 (0.011)	1.8-3.9
	Glyptocephalus zachirus	Rex sole	0.011 (0.002)	-	0.054 (0.005)	5.2-5.9

correlated with axis 3 (r = 0.110). Of the species responses, slender sole and Pacific staghorn sculpin were strongly correlated with axis 2 (r = -0.416, r =

0.406). Two taxa, rockfishes and slender sole, were strongly correlated with axis 1 ($r^2 = 0.538$, $r^2 = -0.487$), while slipskin snailfish were the only species strongly correlated with axis 3 (r = -0.549). There were large overlaps in environmental space when samples were divided by the following grouping factors: season, year, sample depth (m), time of day, latitude, and DO (ml l^{-1}). An MRPP analysis indicated that all grouping factors had a low A-statistic but only five had significant p-values indicating significant differences in species composition of each group within a factor: season ($p < 0.001$), year ($p = 0.002$), depth ($p = 0.015$), time of day ($p = 0.017$), and latitude ($p = 0.002$) (Table 3).

From the ISA, only three factors had significant indicator species for their groups: season, year, and latitude. For the category season, rockfishes, slender sole, butter sole and unidentified right-eyed flatfish (Pleuronectidae) were significant indicators for early (before July 15th) in the season, but there were no significant indicators for late (on/after July 15th) in the season. The category year had one significant indicator species for 2008 (Pacific staghorn sculpin [*Leptocottus armatus*]) and one for 2009 (slender sole). The category latitude had two significant indicator taxa: sculpins (*Artedius* spp.) for the northern sample sites and Pacific staghorn sculpins for the central sample sites.

Ichthyoplankton diversity (H') and evenness (J') varied similarly by year, sample depth (m), time of day, and latitude (Table 4). For year, 2010 had the

Table 3. Multi-Response Permutation Procedures (MRPP) and Indicator Species Analysis (ISA) results for season, year, sample depth (m), day/night, latitude, and dissolved oxygen (ml l^{-1}) differences in the composition of the dominant taxa. Also given are the sample size (n) for each subset of data and the ISA p-values for the significant ($p < 0.05$) taxa.

Factor group	MRPP A-statistic	MRPP p-value	Significant indicator species
Season Early (n=68) Late (n=52)	0.019	<0.001	Early: *Sebastes* spp. (0.034), *L. exilis* (0.046), Unidentified pleuronectidae (0.004), *I. isolepis* (0.003)
Year 2008 (n=39) 2009 (n=27) 2010 (n=54)	0.015	0.002	2008: *L. armatus* (0.012) 2009: *L. exilis* (0.020)
Depth 0.00-24.99 (n=26) 24.99-49.99 (n=66) 50.00-74.99 (n=23) 75.00-99.99 (n=4)	0.013	0.015	None
Time of Day Day (n=95) Night (n=25)	0.008	0.017	None
Latitude South (n=57) Central (n=36) North (n=27)	0.016	0.002	North: *Artedius* spp. (0.040), Central: *L. armatus* (0.037)
Dissolved oxygen 0.00-1.49 (n=3) 1.50-1.99 (n=16) 2.00-2.99 (n=48) 3.00-3.99 (n=25) ≥ 4.00 (n=28)	0.002	0.324	None

Table 4. Taxonomic diversity (H'), evenness (J') and sample size (N) for ichthyoplankton collected along the central Oregon and Washington coasts by season, year, sample depth (m), day/night, latitude and dissolved oxygen (ml l^{-1}).

Category	Category division	H'	J'	N
Season	Early (May-July 14)	0.581	0.783	68
	Late (July 15-Sept.)	0.524	0.646	52
Year	2008	0.398	0.569	39
	2009	0.226	0.296	27
	2010	0.593	0.762	54
Depth	0.00-24.99	0.436	0.635	26
	25.00-49.99	0.576	0.749	66
	50.00-74.99	0.248	0.332	23
	75.00-99.99	0.066	0.044	4
Day/Night	Day	0.741	0.903	95
	Night	0.280	0.383	25
Latitude	North	0.244	0.311	27
	Central	0.423	0.626	36
	South	0.604	0.772	57
Dissolved oxygen	0.00-1.49	0.000	0.000	3
	1.50-1.99	0.240	0.392	16
	2.00-2.99	0.511	0.750	48
	3.00-3.99	0.331	0.498	25
	$\geq$ 4.00	0.336	0.442	28

highest diversity value while 2009 had the lowest diversity value. Although the diversity and evenness analyses only included species collected in more than 3.0% of the samples, the total species catch for 2009 (Table 1) had a much lower percent of samples with fish and a lower number of taxa collected than both 2008 and 2010. The high diversity and evenness in 2010 is most likely the reason there were no indicator species for this year (Table 3) as there were for 2008 and 2009. Similarly, the diversity index was higher for southern sampling sites than either central or northern sampling sites and again, there were no indicator species for southern sampling sites but there were for the central and northern (Table 3). Diversity was also higher in shallower depths (0 – 24.99 m & 24.99 - 49.99 m) than in deeper depths and in samples collected during the day than samples collected at night, but there were no indicator species for these factors.

2.5.2 Horizontal distribution analysis & Individual responses to DO

The best-fitted GAM explained 45.5% of the deviance in observed fish larvae abundance. Bottom-DO had significant positive effects ($p < 0.05$) on larval fish abundance (Fig. 2). Sample locations south of Newport Oregon (southern: 44.00^{o}N - 44.65^{o}N) and samples collected between mid-July and early September, had significantly higher larval fish abundances ($p = 0.007$ and $p < 0.001$, respectively) than samples collected north of Newport (central: 44.65^{o}N – 46.00^{o}N; northern: 46.00^{o}N – 48.00^{o}N) and between late May-mid July (Table 5).

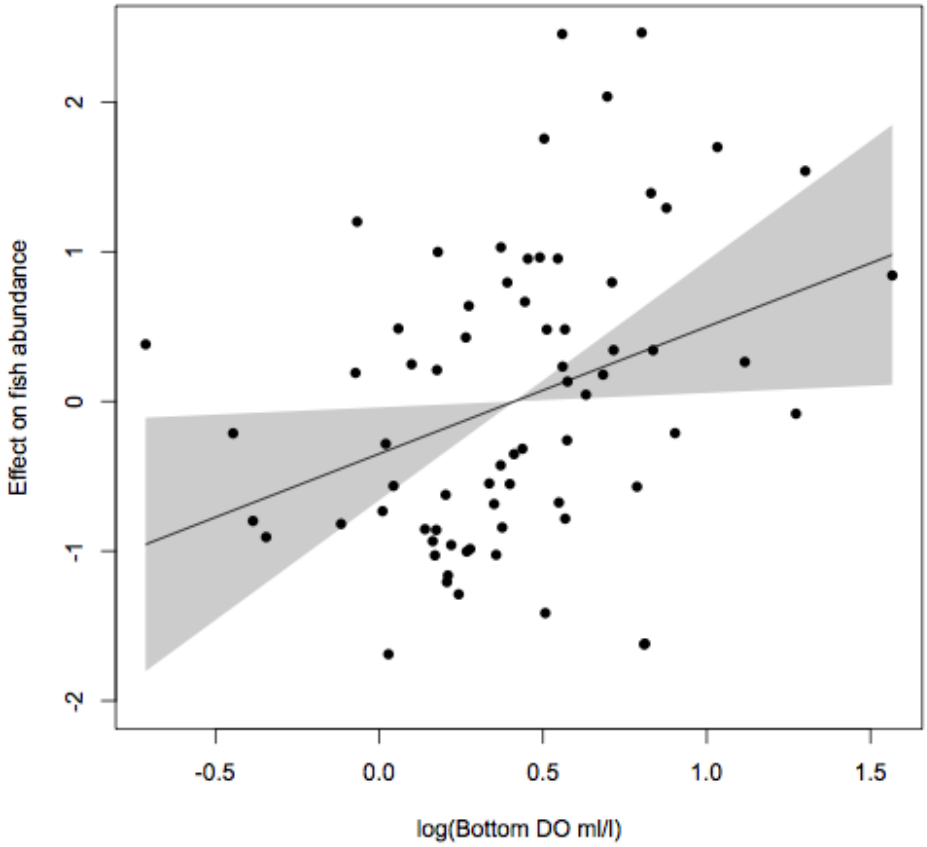

Figure 2. Effects of bottom dissolved oxygen (DO; natural log transformed) on standardized larval fish abundance (natural log transformed) including the 95% confidence interval (shaded area) using the Generalized Additive Model.

Table 5. Generalized Additive Model results for larval fish abundance ((no. m^{-3}), natural log transformed) including sample size (n), generalized cross-validation scores (GCV), deviance explained (Deviance), adjusted *R*-squared value (R-sq (adj.)), Scale estimate (Scale est.); estimate, standard error (Std. Error), t-value, and p-value for the categorical variables; estimated degrees of freedom (edf), ref. degrees of freedom (Ref. df), F-statistic (F), p-value for the continuous variables: bottom dissolved oxygen (DO), sea-surface (SS) salinity and sea-surface (SS) temperature.

Variable	n	GCV	Deviance	R-sq (adj.)
Larval fish abundance (no. m^{-3})	106	0.257	45.50%	0.385

Variable (factor terms)	Estimate	Std. Error	t-value	p-value
Late (Season)	-0.645	0.132	-4.897	<0.001
Day	0.052	0.185	0.276	0.783
Central (Lat.)	0.196	0.136	1.47	0.145
Southern (Lat.)	0.474	0.164	2.89	0.005
Depth 2 (51m -75 m)	0.279	0.169	1.653	0.102
Depth 3 (76 m -100 m)	0.135	0.171	0.791	0.431
Depth 4 (>100 m)	0.191	0.189	1.016	0.312

Variable (smooth terms)	edf	Ref. df	F	p-value
Bottom-DO	2.117	2.713	3.029	0.038
SS Salinity	1.330	1.542	0.270	0.705
SS Temperature	1.495	1.734	0.804	0.435

Of the twelve dominant taxa, only two had significant correlations ($p < 0.10$) between abundance and DO. Slender sole and sand sole had a negative significant correlation with DO ($p = 0.07$ and $p = 0.07$, respectively). Conversely, northern lanternfish (*Stenobrachius leucopsarus*) showed a positive correlation, but this relationship was not significant ($p = 0.10$)

2.5.3 ANOVA and Vertical distribution

Vertical distribution of fish larvae in relation to bottom-DO (ml l^{-1}), differed between day and night samples. During the day, there was a positive significant relationship between the vertical distribution of fish and bottom-DO ($p = 0.037$), which indicated that larvae were lower in the water column (Z_{fi} closer to 0) during the day when bottom-DO was low. There was no significant relationship for species distribution at night. Latitude also had a significant effect on the weighted average depth of fish (Z_{fi}). Samples collected between 44.65^{o}N and 46.00^{o}N had a negative significant relationship ($p = 0.035$) between larval fish vertical distribution and bottom-DO, indicating larval fish in this region were higher in the water column (Z_{fi} closer to 1) when bottom-DO was low. Samples collected in the central region, between 44.65^{o}N and 46.00^{o}N, also had a negative significant relationship between weighted average depth and hypoxia layer thickness ($p = 0.023$), indicating larval fish in this region were higher in the water column when the bottom hypoxic layer was thickest. The results of the Tukey multiple comparison test indicated that the central region differed in fish weighted average depth from the other two regions (vs. north; $p = 0.04$ and vs. south; $p =$

0.055, respectively). None of the twelve dominant taxa, when analyzed individually, showed significant relationships ($p < 0.10$) in their vertical distributions relative to DO or hypoxia layer thickness.

2.6 Discussion

This study provides insight into the effects of DO on larval fish distribution, community composition, and abundance along the Oregon and Washington coasts during the summer upwelling season. The cause of severe hypoxia along the central Oregon coast has been attributed to shelf circulation, shelf productivity and vertical proximity of upwelling source water to the OMZ (Grantham et al. 2004, Chan et al. 2008). Although there were few severe hypoxic values recorded during this study period, during 2002 and 2006 the central Oregon coast became severely hypoxic and even anoxic (2006) for several weeks to months (Chan et al. 2008). Chan et al. (2008) reported that with the onset of anoxia in 2006, severe hypoxia became widespread, at least 3000 km^2, across the central Oregon shelf between 44.25^{o}N and 45.00^{o}N from the innershelf to the shelf break. This hypoxic event also occupied 80% of the water column and persisted from June-October (Chan et al. 2008). Fish larvae that recruit to the central region (44.65^{o}N - 46.00^{o}N), therefore, have a chance of experiencing severe hypoxic and possibly anoxic waters. In response to severe hypoxic and anoxic waters the fish larvae might need to shift their vertical and horizontal distribution to avoid the hypoxic region.

Fish have been observed with stationary hydroacoustics and surface-towed split beam echosounders, moving horizontally and vertically to avoid hypoxic regions (Keister et. al. 2000, Taylor & Rand 2003, Klumb et al. 2004, Bell & Eggleston 2005, Taylor et al. 2007, Parker-Stetter & Horne 2008, Ludsin et al. 2009, Vanderploeg et al. 2009, Zhang et al. 2009). The vertical distribution of fish larvae was not affected by bottom-DO during this study except when I divided the sampling area into three regions: north, central, south. The three regions varied in latitude but also shelf width. The width of the shelf can affect physical and biological dynamics (e.g., circulation, productivity, turbulence, etc.) (Kirincich & Barth 2008, Dudas et al. 2009). For example, the northern region along Washington has a very narrow shelf, while the southern region, around Heceta Bank, has a very wide shelf with greater primary productivity and water retention.

Fish larvae were more abundant in the southern region most likely due to its high productivity and larval fish retention caused by ocean circulation patterns across the wide shelf, particularly on Heceta Bank (Kirincich & Barth 2008). For samples collected from the central region, between 44.65^{o}N and 46.00^{o}N (roughly corresponding from Newport to Astoria, Oregon), larval fish were shallower in the water column when bottom-DO was lowest. Larval fish distribution was also shallower in the water column when the hypoxic layer was thickest in the 'central' region. The thickness of the hypoxic layer is an indicator of quality habitat available for pelagic fish larvae. As the hypoxic layer thickness increases, less suitable habitat is available for pelagic fish larvae. A reduction in available habitat

can cause an increase in local fish densities in shallow waters and may increase the competition for limited prey resources as well as increase the risk of predation (Taylor & Rand 2003, Herbert et al. 2010, McClatchie et al. 2010, Koslow et al. 2011). Zhang et al. (2009) found that when habitat quality was reduced for pelagic fish during years of severe hypoxia, the fish tended to aggregate horizontally along and above the edges of the hypoxic region. Prince & Goodyear (2006) also found that the distribution of tropical pelagic fish (Atlantic blue and white marlins (*Makaira nigricans* and *Tetrapturus albidus*), Atlantic sailfish (*Istiophorus platypterus*), etc.) was reduced to a narrow surface layer due to a thick hypoxic layer. The central Oregon coast has been the main area of concern among scientists in the last decade for severe hypoxic events. Therefore, with the evidence presented in this study of larval fish habitat suppression when bottom-DO is low or the hypoxic layer thickness increases, it is important to continue to monitor the success of larval fish recruitment during the hypoxic season. If the number of larval fish recruits is reduced due to predation or prey limitation from habitat suppression, in two or more years, there could be a subsequent reduction in adult populations.

I did not find major impacts of DO on larval fish distribution and community composition – a result that contrasts previous studies conducted in enclosed basins (Breitburg 2002, Taylor & Rand 2003, Vanderploeg et al. 2009). This would seem to indicate that during most years, the larval fish community composition along the Oregon and Washington coasts are more influenced by

other oceanographic variables (e.g., depth, upwelling intensity, wind stress, circulation patterns, etc.) rather than DO (Barth et al. 2007, Dudas et al. 2009). Also, the timing of this study appears to coincide with an increase of DO in the Pacific Ocean according to Whitney et al. (2007). Whitney et al. (2007) identified a 18.6-year cycle for DO in the North Pacific Ocean, that has the most recent low period occurring between 2002 and 2006, which coincides with the lowest DO values recorded recently along the central Oregon Coast (Grantham et al. 2004, Chan et al. 2008, Pierce et al. 2012). However, Whitney et al. (2007) recognized that this cycle was due to subarctic water influences while the central Oregon and Washington coast upwelling is sourced by both subarctic and equatorial waters (Thomson & Krassovski 2010). The DO cycle defined by Whitney et al. (2007) could have long-lasting effects on the recruitment of fish larvae along the Oregon and Washington Coasts during the summer upwelling season. Fish recruiting during the upwelling season are typically spawned during the winter or early spring (e.g., rockfishes (*Sebastes* spp.), rex sole (*Glyptocephalus zachirus*), slender sole (*Lyopsetta exilis*), etc) (Matarese et al. 1989). Thus long-term monitoring will provide a better understanding of the impacts hypoxia is having on this region's local ecosystem and important marine fish species (Keller et al. 2010, McClatchie et al. 2011).

2.7 References

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CHAPTER 3: Interannual and seasonal variability of the distribution and abundance of benthic fishes in nearshore waters off central Oregon

3.1 Abstract

Nearshore central Oregon waters provide necessary juvenile settlement habitat for a variety of fishes including commercially important flatfishes and rockfishes. Previous studies from the 1970's and early 1980's have shown that fish species abundance, length and distribution are strongly correlated with depth and sediment type for this area but these studies did not investigate the influence of bottom dissolved oxygen (DO) on the above fish species metrics. In this study, I investigated the relationship between species composition, abundance, length, and body condition to bottom depth, bottom temperature and bottom-DO. I focused the sampling efforts off Moolack Beach, Oregon at sample locations less than 100 m depth that have a mostly sandy bottom. Sampling occurred during the summers of 2008 - 2011. English sole (*Parophrys vetulus*), butter sole (*Isopsetta isolepis*), speckled sanddab (*Citharichthys stigmaeus*) and Pacific sanddab (*Citharichthys sordidus*) dominated the catch. However, the dominant species shifted between years, with butter sole dominating the catch in 2008 and 2009 and speckled sanddab dominating the catch in 2010 and 2011. A relationship was identified between species composition, abundance and length with respect to depth. Specifically, I found that English sole, butter sole and speckled sanddab were more abundant and smaller at nearshore (30 m) stations than offshore (80 m) stations,

whereas Pacific sanddab were more abundant offshore but did not significantly differ in size between stations. Bottom-DO had significant relationships with small English sole (< 75 mm), small speckled sanddab (<100 mm) and Pacific sanddab abundance as well as a negative effect on the body condition of small butter sole (< 75 mm). These results, add to those from previous studies by showing that bottom-DO may also affect juvenile fish distribution in this region. However, many co-varying factors, such as temperature and depth may also be important in driving the observed changes.

3.2 Introduction

The nearshore waters (< 100 m) of the central Oregon coast, particularly off Moolack Beach, are composed mostly of sandy bottoms with a few rocky outcroppings (Romsos et al. 2007). Pearcy (1978) and Wakefield (1984) have shown that the area is biologically rich and dominated by Pacific sanddab (*Citharichthys sordidus*), sand sole (*Psettichthys melanostictus*), speckled sanddab (*Citharichthys stigmaeus*) and Pacific tomcod (*Microgadus proximus*). Many of the species in this region vary in life history strategies and feeding habits to create a very complex and dynamic ecosystem (Kravitz & Pearcy 1976, Wakefield 1984).

The central Oregon coast is also a physically and chemically dynamic location with strong summer upwelling and hypoxic events. In central Oregon, hypoxic levels (<1.4 ml l^{-1}) have been documented annually along the inner-shelf (< 50 m) since 2000 (Grantham et al. 2004, Chan et al. 2008, Pierce et al. 2012). Variations in hypoxia occur both spatially, vertically and horizontally, and

temporally along the inner-shelf. Many studies have focused on the tolerance of benthic organisms to low dissolved oxygen (DO) (Diaz & Rosenberg 1995, Miller et al. 2002, Altieri 2008, Vaquer-Sunyer & Duarte 2008, Zhang et al. 2010), but few studies have investigated the effects of low DO on early life stages in upwelling-driven systems (e.g., the central Oregon coast).

Organisms, such as juvenile flatfish, may change their association with the sedimentary environment or move into the water column to find higher DO concentrations. Physiological stress and vulnerability to predation may increase while growth rates and habitat space may be reduced, ultimately increasing mortality, with these changes in fish behavior and habitat associations (Chabot & Dutil 1999, Tallqvist et al. 1999, Breitburg 2002, Gray et al. 2002, Rabalais et al. 2002, Wu 2002, Bell & Eggleston 2005). The level of DO that begins to cause physiological and behavioral changes in various organisms differs, but effects have been shown to occur when DO drops below 1.4 ml l^{-1} (Diaz 2001, Vaquer-Sunyer & Duarte 2008), which is considered the threshold for hypoxic levels. Areas susceptible to coastal upwelling, and thus hypoxic events, might experience community shifts and changes of trophic interactions due to the various degrees of species tolerance to low DO levels.

The central Oregon coast is also an area of interest because of its selection as the location of the Northwest National Marine Renewable Energy Center Ocean Test Berths off of Newport, Oregon (Boehlert et al. 2008, Brekken et al. 2009). The test berths have three anchors that rest on the seafloor with 100 m between

anchors. Each anchor roughly covers a 6 x 6 x 3 m area (Boehlert et al. 2008). The location of the test berths is within my study area, just off of Moolack Beach, Oregon. Just south of the sampling area is also the disposal site for dredge spoils from Yaquina Bay, a major Oregon seaport. The potential effects of both the influx of sand from the dredge and the addition of a bottom structure from the wave energy test facility to this region increase the need for understanding the benthic ecosystem in this area.

In this study, I investigated the effects of environmental variability on juvenile fish. I sampled during the summer upwelling season from 2008 to 2011 and explored relationships between abiotic parameters (i.e. bottom depth, bottom-DO and bottom temperature) and community composition, species abundance (for the dominant species), species length (for English sole (*Parophrys vetulus*), butter sole (*Isopsetta isolepis*), Pacific sanddab and speckled sanddab) and fish body condition (for English sole, butter sole and speckled sanddab). Results from this study are expected to provide an understanding of the community structure and distribution of newly settled fish, and the effects of hypoxia on the abundance and distribution of juvenile fish. Fisheries managers will then be able to utilize these results when trying to identify the success of the economically and commercially important fish cohorts settling during strong hypoxic conditions.

3.3 Methods

I collected a total of 92 samples from the summers of 2008-2011 (2008 = 16, 2009 = 5, 2010 = 27, 2011 = 44) at ten stations along, north and south of the

historic Newport Hydrographic line (Fig. 3). Two stations were located along the historic Newport Hydrographic Line (~ 44.66^{o}N) at 55 m and 80 m depth and two stations were located slightly north of the Newport Hydrographic Line at 30 m and 40 m. These stations were named Moolack Beach 30 m (MB30), Moolack Beach 40 m (MB40), NH5 (55 m) and NH10 (80 m) (Fig. 3). Six additional stations formed a grid both north (N) and south (S) of the Newport Hydrographic line ranging form 30 m to 55 m depth (Fig. 3). These six stations were added in 2010 to include the area where the wave energy test berths will be located. I collected fish using a 2.0 m-wide beam trawl constructed of 38-mm mesh (stretch measure) and lined throughout with 3-mm mesh (diameter measure). A tickler chain was attached to the beam trawl skids forward of the trawl footrope. Tows were 10 min long from the end of wire out to the start of the wire retrieval (assumed to be bottom contact time). An odometer wheel (radius = 1.38 cm) with a counter to record the number of revolutions during each tow was attached to one skid. I quickly sorted catches at sea by major taxa (e.g., flatfish, roundfish, and fish < 15 cm) and immediately froze the catch on dry ice. In the laboratory, I thawed the catch, identified the catch to species, and weighed (g) and measured (total length (TL) = mm) each fish. A CTD (Conductivity-Temperature-Depth) (Sea-Bird Model 25 with a flow-through DO sensor) cast was made at the starting point of each tow to measure the salinity, temperature, and bottom-DO.

3.3.1 Environmental Relationships

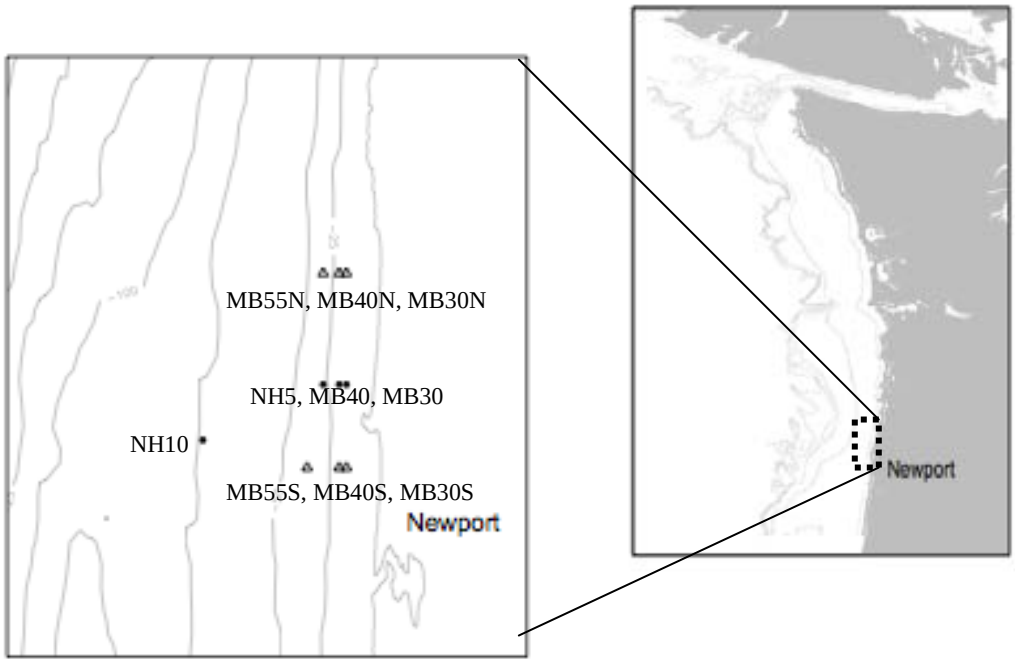


Figure 3. Maps of the sample survey area. The filled circles (NH10, NH5, MB40, MB30) represent the sample stations for 2008 and 2009, while the open triangles (MB55N, MB40N, MB30N, MB55S, MB40S, MB30S) represent the stations added in 2010 and 2011.

I conducted a non-metric multidimensional scaling (NMS) analysis, using PC-Ord v.6, to determine if a relationship occurred between fish community structure and environmental parameters. A Bray-Curtis distance measure was used with random starting configurations. I only included species/groups that occurred in more than 3.0% of the samples in the species matrix, for a total of 28 species/groups in the primary matrix with 92 sample units (Table 6). Each sample unit represented one tow of the beam trawl. Tow area (m^2) was used to standardize the species counts. I calculated the tow area from the circumference of the odometer wheel, the number of revolutions recorded on the odometer counter, the number of ticks it takes to make one revolution on the odometer counter, and the distance between the skids (Carey and Heyamoto 1972, Pearcy 1978). The environmental parameters I used in this analysis included bottom depth, bottom-DO, and bottom temperature. Three categorical variables were included in the environmental parameter matrix as well: time of day, season and year. I divided the category, time of day, into two groups: day (from sunrise to sunset) and night (from sunset to sunrise). The majority of the tows were conducted between sunrise and sunset, with night sampling occurring in 2008 and 2011 only. I divided the category season into three groups: early (May – June), mid (July – end of July), to late (August-September). The season categories were chosen based on the timing of recruitment for dominant species to the sample area (e.g., English sole), and the timing of upwelling-induced hypoxia (Boehlert & Mundy 1987, Gunderson et al. 1990, Barth et al. 2007).

Table 6. The abbreviated names for species used in the non-multidimensional analysis (NMS).

Species		Abbreviated name
English sole	*Parophrys vetulus*	E.sole
Butter sole	*Isopsetta isolepis*	B.sole
Pacific sanddab	*Citharichthys sordidus*	P.sandda
Speckled sanddab	*Citharichthys stigmaeus*	S.sandda
Slender sole	*Lyopsetta exilis*	Sl.sole
Dover sole	*Microstomus pacificus*	D.sole
Sand sole	*Psettichthys malanostictus*	Sa.sole
Unidentified sanddab	*Citharichthys* spp.	Sanddab
Petrale sole	*Eopsetta jordani*	Pt.sole
Rex sole	*Glyptocephalus zachirus*	R.sole
Pacific sandlance	*Ammodytes hexapterus*	P.sandla
Warty poacher	*Ocella verrucosa*	W.poache
Tubenose poacher	*Pallasina barbata*	T.poache
Pygmy poacher	*Odontopyxis trispinosa*	Py.poach
Pacific tomcod	*Microgadus proximus*	P.tomcod
Smelts	Osmeridae	Osmerids
Pacific lingcod	*Ophidon elongatus*	Lingcod
Alligatorfish	*Aspidophoroides monopterygius*	Alligato
Thornback sculpin	*Paricelinus hopliticus*	Tb.sculp
Roughback sculpin	*Chitonotus pugetensis*	Rb.scul
Pacific staghorn sculpin	*Leptocottus armatus*	Pst.scul
Unidentified sculpin	Cottidae	Sculpin
Unidentified rockfish	*Sebastes* spp.	Rockfish
Prickleback	Stichaeidae	Prk.back
Big skate	*Raja binoculata*	Big.Skte
Canary rockfish	*Sebastes pinniger*	Can.Rock
Snake prickleback	*Lumpenus sagitta*	Snk.prk
Snailfish	*Liparis* spp.	Snailfis

3.3.2. Abundance and Length Analysis

I related bottom-DO values to species counts for the four dominant species (English sole <75 mm, butter sole <75 mm, speckled sanddab <100 mm and Pacific sanddab all sizes) with a generalized additive model (GAM, Wood 2008) in the statistical package *R* v. 2.10.1 (The R Foundation for Statistical Computing, http://www.r-project.org). A GAM is a non-parametric regression model that does not require *a priori* specification of the functional relationship between the independent and dependent variables (Wood 2006). A poisson family distribution and a log link function were used to account for the skewness of the distribution brought on by the abundant zero catch data points. In this GAM, I offset species counts by the natural log of the sample area using the "offset" term in *R*, while bottom-DO values were natural log-transformed. I also included the factors year, season and depth category in the GAM. The groups within the factors season and year were the same as used in the NMS analysis, while the factor depth was divided into four groups matching the depths of the sample stations: 30 m, 40 m, 55 m, and 80 m. The size classes for each species were chosen to target the newest recruits (recently settled fish).

I compared the average total lengths of the four dominant species to station depth (by category) using both an ANOVA and Tukey multiple comparison test. Each average length measurement from each station was weighted by the species abundance at that station within the ANOVA model. All univariate and

multivariate analyses described above were conducted with the statistical package *R* v.64.

3.3.3 Body Condition Analysis

I investigate the impact of bottom-DO values to the body mass index (BMI) for two different size classes of three species: English sole (< 75 mm & ≥75 mm), butter sole (< 75 mm & ≥75 mm) and speckled sanddab (<100 mm & ≥100 mm). The three species were chosen due to their dominance in the catch data, while the size classes for each species were chosen to target the newly settled fish. First, I calculated the BMI, or condition index, by taking the residuals from the species length (total length) versus species weight using a GAM with a Gaussian family model and identity link function. Each species' total lengths (F_{Li}) and weights (F_{Wi}) were natural log-transformed to meet the constant variance assumption. The "s" in the GAM below represented a smoothing function.

$$\log(F_{Wi}) \sim s(\log(F_{Li}) + e)$$

Next, I correlated the residuals, or condition index, from the GAM to the continuous variable bottom-DO, the categorical variables season, year, and station depth; and the interaction variables bottom-DOxseason, and bottom-DOxstation depth using an Analysis of Covariance (ANCOVA) model with a backward variable selection strategy. The category season was divided into the same three groups used in the NMS analysis: early (May – June), middle (July – end of July), and late (August-September). The category station depth was also divided into the same groups used in the previous ANOVA model: 30 m, 40 m, 55 m, and 80 m.

3.4 Results

Bottom-DO ranged from 0.90 – 8.11 ml l^{-1} over all four years. The value 8.11 ml l^{-1} was only measured on one occasion and was confirmed as a correct measurement by correlating the bottom-DO values to the bottom temperature and bottom salinity values from the same CTD cast. The next highest bottom-DO value measured over all four years was 5.22 ml l^{-1}. Mean bottom-DO from each station varied interannually and seasonally (Fig. 4a). Mean bottom-DO for each year varied with depth, with lower and less variable values at deeper stations (Fig. 4b). Only 12 stations had mean bottom-DO values at or below hypoxic values (1.4 ml l^{-1}) either interannually or seasonally. Three of those events were recorded from the 80 m station, four from the 55 m and the 40 m stations, and one from the 30 m station. No hypoxic values were recorded in 2011, nor were any hypoxic values recorded before July 1st.

English sole, butter sole, Pacific sanddab and speckled sanddab were the four dominant species across all sampled years (Table 7). Species abundance, however, varied from year to year. Butter sole were the most abundant species in 2008 and 2009, closely followed by English sole in 2008. Speckled sanddab was the most abundant species in 2010 and 2011 (Table 7).

3.4.1 Environmental Relationships

The NMS model suggested a three axes solution with a final stress of 11.63 (Fig. 5). The cumulative variance explained by all three axes was r^2=0.874, with axis 1 explaining the most variance at r^2=0.540, axis 2 at r^2=0.206 and axis 3 at

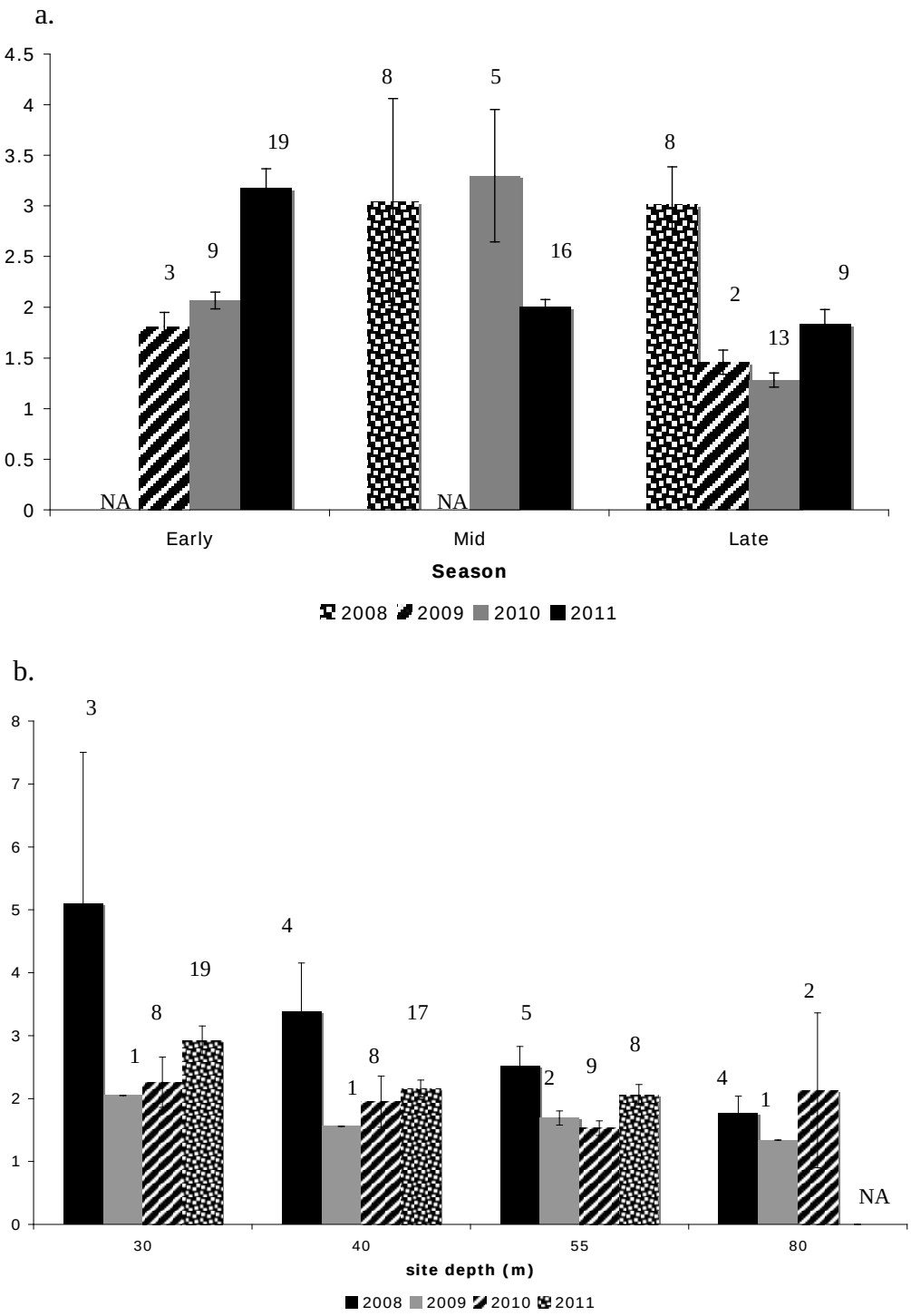


Figure 4. Bar plots of mean bottom-DO and standard error bars for a) season within a sample year (early: May - June; mid: July; late: Aug. - Sept.) and b) site depth for each sample year. The numbers above the bars represent the sample size (n).

Table 7. Mean standardized species abundance ((fish m^{-2})*100) for each species or group by sample year (n=92 stations). Standard deviation included in parenthesis.

Species	2008	2009	2010	2011
Butter sole *Isopsetta isolepis*	9.31 (0.2122)	18.88 (0.3772)	4.02 (0.0842)	4.82 (0.0577)
English sole *Parophrys vetulus*	8.79 (0.1435)	10.16 (0.0975)	3.93 (0.0455)	7.21 (0.1085)
Pacific sanddab *Citharichthys sordidus*	3.93 (0.0402)	3.89 (0.0505)	2.23 (0.0307)	0.30 (0.0083)
Speckled sanddab *Citharichthys stigmaeus*	3.02 (0.0362)	2.51 (0.0175)	8.91 (0.0749)	9.67 (0.0800)
Pacific sand lance *Ammodytes hexapterus*	1.46 (0.0321)	0.04 (0.0008)	0.11 (0.0032)	0.01 (0.0005)
Slender sole *Lyopsetta exilis*	0.07 (0.0018)	0.19 (0.0026)	0.06 (0.0019)	0.00 (0.0000)
Dover sole *Microstomus pacificus*	0.09 (0.0016)	0.10 (0.0010)	0.04 (0.0015)	0.04 (0.0012)
Sand sole *Psettichthys malanostictus*	0.03 (0.0011)	0.04 (0.0008)	0.17 (0.0035)	0.52 (0.0098)
Unidentified Sanddab *Citharichthys* spp.	0.09 (0.0033)	-	0.62 (0.0130)	1.36 (0.0254)
Petrale sole *Eopsetta jordani*	0.02 (0.0006)	-	0.01 (0.0004)	-
Rex sole *Glyptocephalus zachirus*	0.01 (0.0004)	-	-	0.08 (0.0032)
Warty Poacher *Ocella verrucosa*	0.19 (0.0039)	0.05 (0.0012)	0.65 (0.0293)	0.05 (0.0013)
Tubenose poacher *Pallasina barbata*	0.10 (0.0027)	0.10 (0.0023)	0.08 (0.0024)	0.05 (0.0028)
Pygmy poacher *Odontopyxis trispinosa*	-	-	0.02 (0.0006)	0.04 (0.0016)
Pacific tomcod *Microgadus proximus*	0.99 (0.0159)	0.14 (0.0021)	0.01 (0.0005)	0.07 (0.0018)
Smelts Osmeridae	0.02 (0.0007)	0.08 (0.0017)	0.19 (0.0069)	0.82 (0.0313)
Pacific lingcod *Ophidon elongates*	0.11 (0.0037)	-	-	0.03 (0.0018)
Alligatorfish *Aspidophoroides monopterygius*	-	-	0.01 (0.0005)	-
Thornback sculpin *Paricelinus hopliticus*	0.01 (0.0003)	-	0.03 (0.0010)	-

Table 7 (continued).

Species	2008	2009	2010	2011
Roughback sculpin *Chitonotus pugetensis*	0.12 (0.0027)	0.33 (0.0075)	0.02 (0.0011)	0.03 (0.0012)
Pacific staghorn sculpin *Leptocottus armatus*	0.30 (0.0045)	0.18 (0.0041)		0.15 (0.0034)
Sculpins Cottidae unidentified	0.22 (0.0046)	-		-
Rockfishes *Sebastes* spp.	0.06 (0.0017)	-	0.22 (0.0055)	0.02 (0.0006)
Big skate *Raja binoculata*	0.001 (0.0019)	-	-	-
Canary rockfish *Sebastes pinniger*	0.08 (0.0013)	-	-	0.03 (0.0009)
Snake prickleback *Lumpenus sagitta*	0.03 (0.0000)	-	0.01 (0.0000)	0.02 (0.0010)
Snailfishes *Liparis* spp.	_	_	_	0.01 (0.0027)

Figure 5. The relationship between the three environmental parameters (vectors), Bottom Depth, Bottom Dissolved Oxygen and Bottom Temperature, and species distribution are demonstrated on this 2D Non-Multidimensional Scaling Analysis (NMS) plot along Axes 1 and 2. Final stress for this model was 11.63.

r^2=0.128. Of the environmental parameters examined, bottom depth was most strongly, but negatively, correlated with axis 1 (r = -0.747), but bottom temperature and bottom-DO were also strongly, but positively, correlated with axis 1 (r = 0.364 and r = 0.258, respectively). None of the three continuous variables were strongly correlated with axis 2 or axis 3. However, there appears to be a strong association between the species distribution within the model and axis 2. The factor or variable driving the spread of species along axis 2 is unclear based on the factor/variables included in the model. For the species/groups, butter sole and speckled sanddab were strongly (r > 0.500) correlated with axis 1 (Table 8) while speckled sanddab was also strongly but negatively correlated with axis 2. None of the species were strongly correlated with axis 3 (Table 8), which is why only a 2-Dimensional figure with axis 1 and axis 2 (Fig. 5) was used to show the species spread in environmental space.

3.4.2 Abundance and Length Analysis

Three of the dominant species had a significant relationship between species counts and bottom-DO (Fig. 6). Depth category had a significant relationship with the counts of all four species, while year had a significant relationship with only three species and season only one species (Fig. 7a-c). English sole and butter sole were more abundant in the shallow stations 30 m and 40 m, while Pacific sanddab were more abundant in the deeper stations 55 m and 80 m (Fig. 7a). Speckled sanddab were about equal in abundance at 30 m, 40 m, and 55 m but lower at 80 m (Fig. 7a).

Table 8. Correlation (*r*) values for the top 11 of 28 species, using fish of all sizes caught, from the Non-metric Multidimensional Scaling analysis. (*) denotes which species are strongly correlated (p > 0.500) with each axis.

Species	Axis 1	Axis 2	Axis 3
English sole	0.489	-0.275	-0.482
Butter sole	*0.521	0.240	-0.429
Speckled sanddab	*0.664	*-0.502	0.106
Pacific sanddab	-0.436	-0.491	0.120
Sand sole	0.307	0.068	0.089
Pacific sand lance	0.039	0.019	-0.229
Warty Poacher	0.187	0.053	-0.045
Pacific tomcod	0.091	0.053	-0.388
Smelts	0.194	0.176	-0.191
Pacific staghorn sculpin	0.175	-0.264	-0.103

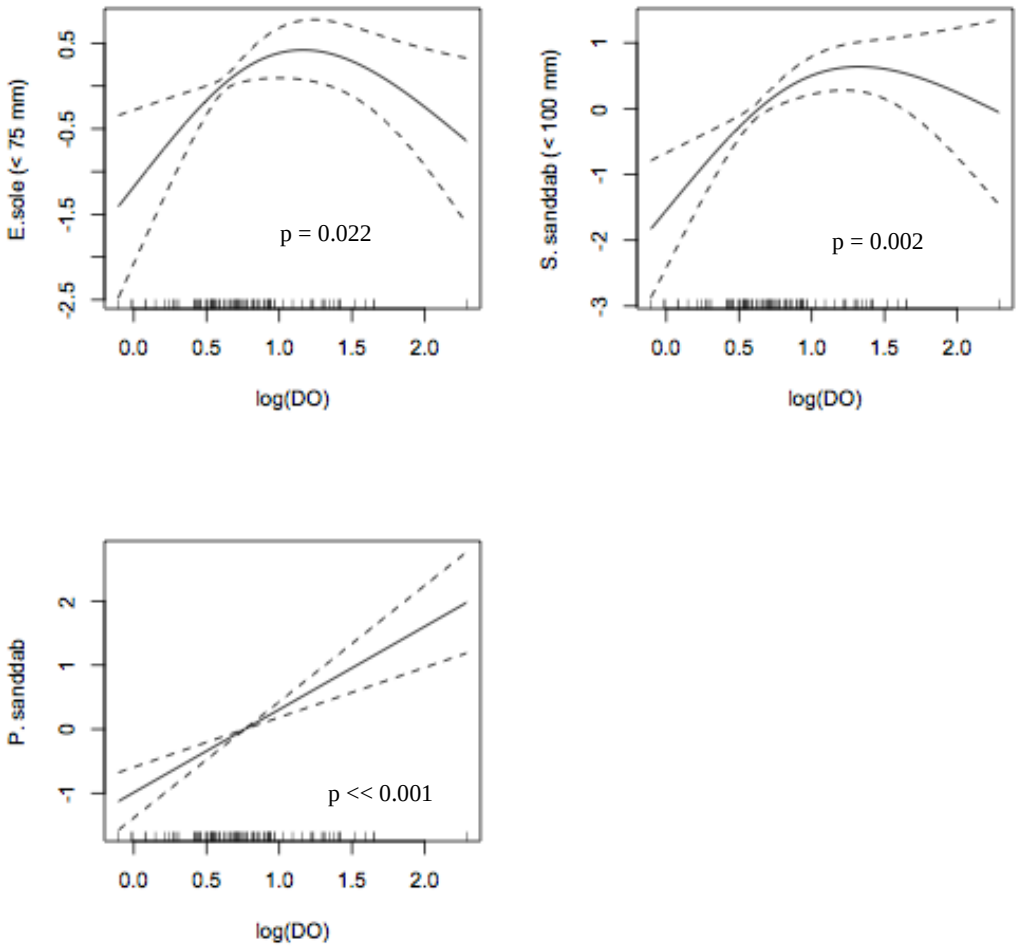
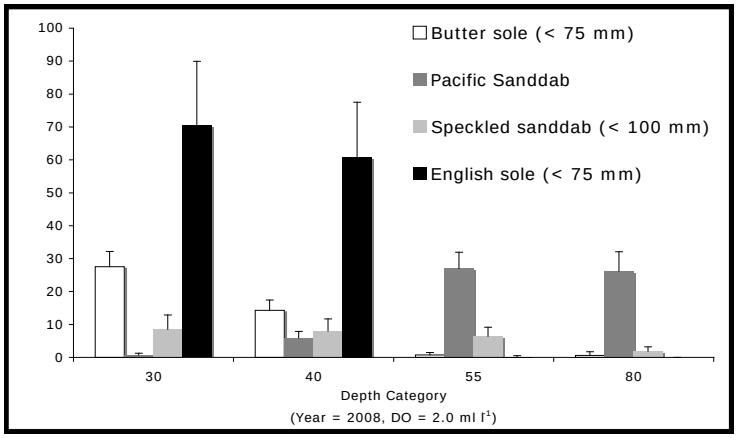
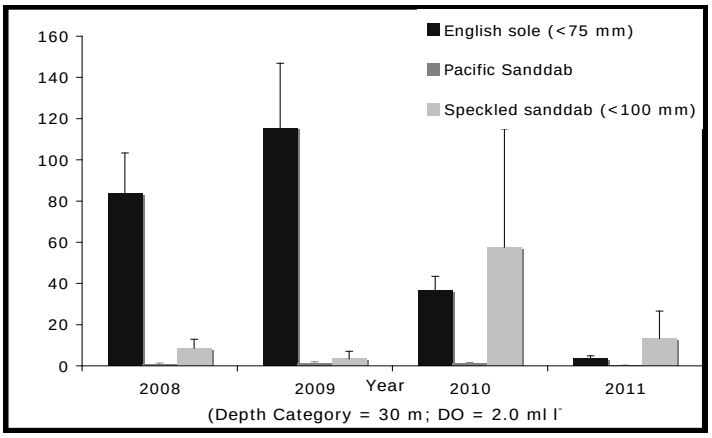


Figure 6. The relationship of species counts to bottom dissolved oxygen as determined from a generalized additive model (GAM) for English sole (< 75 mm), speckled sanddab (< 100 mm) and Pacific sanddab.

a.



b.



c.

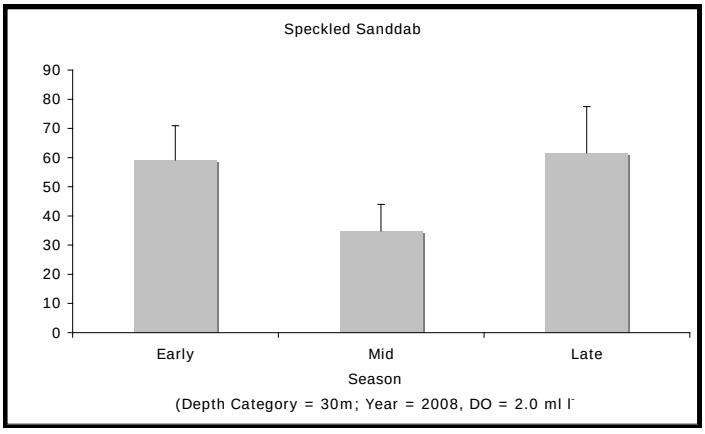


Figure 7. The relationship of species counts to a) depth category, b) year and c) season as predicted from a generalized additive model (GAM) for Pacific sanddab, English sole (< 75 mm), butter sole (< 75 mm) and speckled sanddab (< 100 mm).

The years 2008 and 2009 are marked by high abundance for English sole, while 2010 was characterized by abundance for speckled sanddab (Fig. 7b). Pacific sanddab were most abundant in 2009 (Fig. 7b). Speckled sanddab were least abundant during the middle part of the sample season (Fig. 7c).

The four species were varied in the range of lengths observed during the four years. Both English sole and butter sole had the greatest ranges (21.2-219.0 mm and 20.5-280.0 mm, respectively) while speckled sanddab had the smallest range (51.4-147.0 mm). English sole, butter sole, and speckled sanddab had significant relationships between average total length (mm) and site depth (Fig. 8). For English sole, there was a clear trend of an increase in average total length with increasing site depth. Butter sole had a similar trend to that seen with English sole, except for a decrease in length at the deep station (80 m). For speckled sanddab, a significant difference between stations occurred between the 30 m and 40 m station with smaller fish collected at the 30 m station. For Pacific sanddab, there was no significant relationship between average total length (mm) and site depth ($p = 0.263$).

3.4.3 Body Condition Analysis

The results of the body condition index (BMI) analyses varied between species and among species' size classes. For the smaller fish (i.e. new recruits) examined, only butter sole (< 75 mm) condition index had a significant relationship with environmental variables in the ANCOVA model including year,

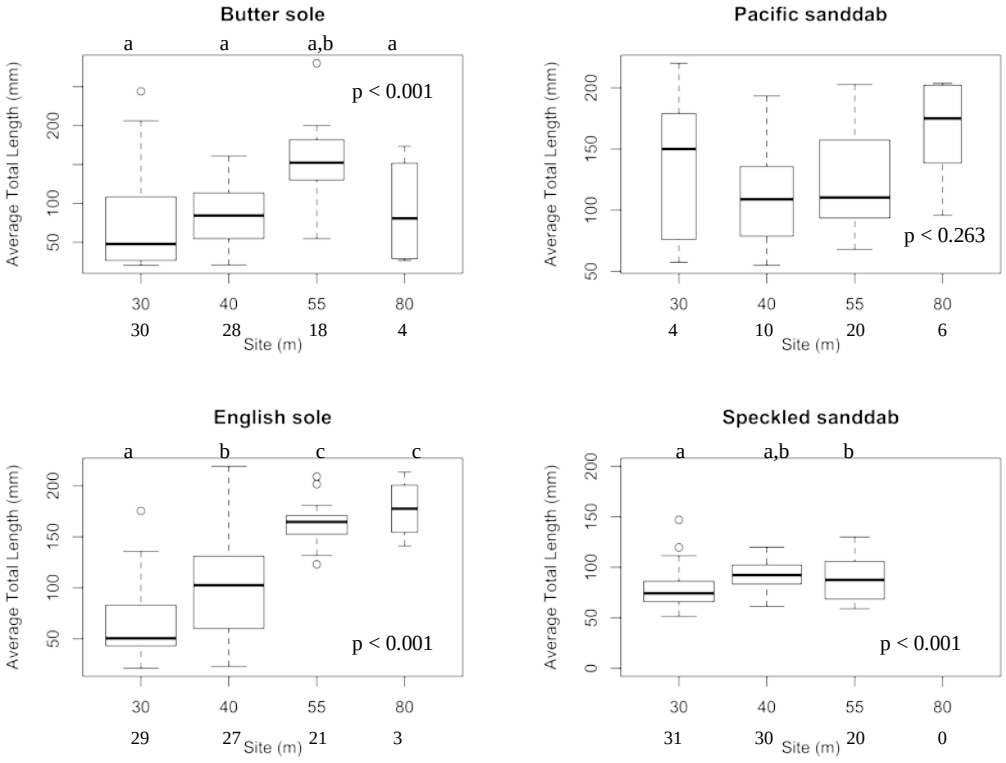


Figure 8. Box plots of fish average length (mm) per sample station category 30 m, 40 m, 55 m, and 80 m. Included are the p-values from an ANOVA and lower-case letters (a, b, and c) represent significant differences among site categories based on a Tukey multiple comparison test. The width of each bar represents the sample size, which is denoted below the station category name.

season, station depth and bottom-DOxstation depth (Table 9). The body condition of small butter sole was significantly greater in 2008 than in the other three years ($p = 0.007$) and was significantly greater in the early part of the season and lower in the mid part of the season ($p = 0.007, < 0.001, 0.005$; early, mid, late). Small butter sole body condition was also significantly greater at the site depth 55 m than 30 m ($p < 0.001$) when bottom-DO was low. Small butter sole had a significant relationship between body condition and bottom-DO with a decrease in the condition index when bottom-DO increased.

For the larger fishes examined, large speckled sanddab (≥ 100 mm) had significant relationships between body condition and season, station depth and bottom-DO (Table 9). The body condition of large speckled sanddab was significantly greater at station depth 30 m than station depth 55 m. Large speckled sanddab body condition was negatively associated with bottom-DO ($p < 0.001$) and increased throughout the sample season (Fig. 9). Large English sole (≥ 75 mm) body condition was significantly related with year, season and station depth. The body condition of large English sole was significantly greater in 2009 than in 2008 ($p = 0.018$) and at station depth 55 m than 30 m ($p = 0.026$). Large English sole body condition increased throughout the sample season (significantly lower in the early part of the season; $p = 0.005$). Large butter sole (≥ 75 mm) body condition was only significantly correlated with year in the ANCOVA model and was significantly lower in 2011 than 2008 ($p = 0.026$). Overall, the relationship

Table 9. ANCOVA model p-values for the body mass index (BMI) of English sole, butter sole and speckled sanddab, for two size classes. NS stands for "not significant" or p-values ≥ 0.05.

	Categorical variables			Continuous Variable	Interaction terms	
	Year	Season	Station Depth	Bottom DO	Bottom DO:Season	Bottom DO:Station Depth
Small Fish						
English sole (< 75 mm)	NS	NS	NS	NS	NS	NS
Butter sole (< 75 mm)	0.042	0.036	< 0.001	NS	NS	< 0.001
Speckled sanddab (< 100 mm)	NS	NS	NS	NS	NS	NS
Large Fish						
English sole (≥ 75 mm)	0.024	0.038	0.013	NS	NS	NS
Butter sole (≥ 75 mm)	0.001	NS	NS	NS	NS	NS
Speckled sanddab (≥ 100 mm)	NS	< 0.001	0.01	0.002	0.003	NS

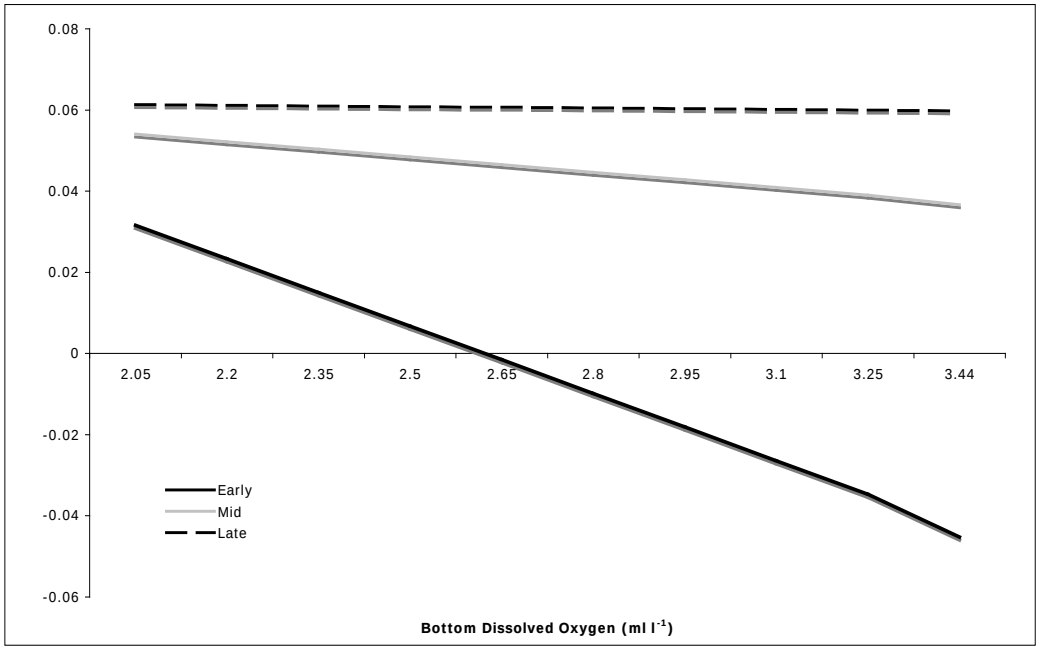


Figure 9. Predicted Body Mass Indexes (BMI) (i.e. condition indexes) for speckled sanddab (≥ 100 mm) vs. bottom-DO for the three season categories (Early: May-June; Mid: July – end of July; Late: August-September) at station depth 30 m.

between body condition index and bottom-DO was species and size dependent.

3.5 Discussion

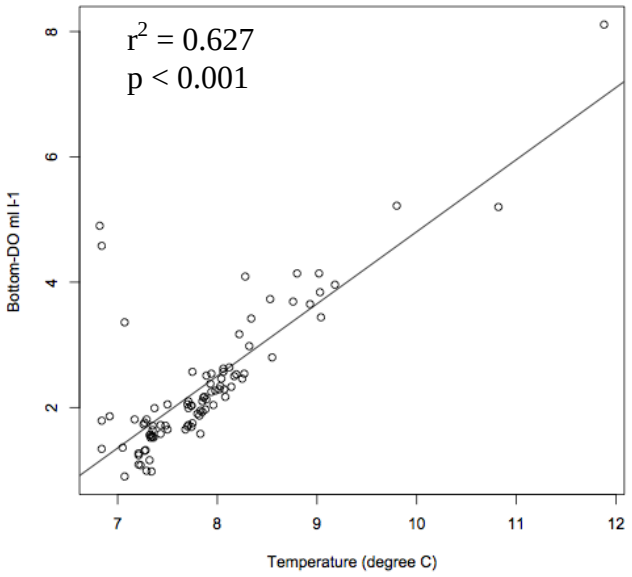
The central Oregon coast is known for strong upwelling and severe hypoxia between late April and early October (Grantham et al. 2004, Barth et al. 2007, Chan et al. 2008). Fluctuations in bottom-DO in this area were highly variable interannually and seasonally, most likely due to variations in oceanographic variables such as wind intensity and upwelling index. I saw very minimal effects of mean seasonal bottom-DO values on species composition. I did see some effects of bottom-DO on the abundance and body condition of the dominant species. However, I did not sample during many hypoxic events nor was I able to continuously monitor the oxygen conditions and fish assemblages over time and space. With my sampling strategy, I was only able to sample isolated events throughout the upwelling and hypoxic season. Juvenile fishes are developed enough to swim, and therefore, are capable of moving in and out of areas with hypoxic conditions. Comparing species abundance and body condition to bottom-DO is therefore complicated without knowing the extent these fish were exposed to hypoxic conditions. However, the distance and extent to which the fishes swim is dependent on fish size/age and on the extent of the hypoxic zone. I focused my comparison on newly settled fish, assuming that the distance these fish would swim would not extend beyond the hypoxic conditions, which have been recorded to expand an area as large as 3000 km^2 (Chan et al. 2008). Also bottom-temperature and bottom depth were correlated with bottom-DO (Fig. 10) and

therefore either low bottom-temperature or depth may mask the effect of low bottom-DO.

In this study, I found that species composition, abundance, and length varied with depth, creating a cross-shelf gradient of species composition, abundance and length. Figure 11 conceptualizes the changes in abundance and length for the dominant species of this study in relation to depth. Specifically, the 30 m station appears to be suitable habitat for newly settled English sole, butter sole and speckled sanddab. Similar to the results of this study, previous studies conducted about 30 years ago found that Pacific sanddab dominated the catch at the mid-shelf (~ 70 m) (Kravitz & Pearcy 1976, Pearcy 1978, Wakefield 1984). More recently, Toole et al. (2011) also identified that species assemblages were structured primarily by depth, with mid-shelf stations dominated by flatfishes. The correlation between abundance and depth for the juveniles also appears to mimic the distribution of the adults for certain species (Allen & Pondella 2006). For instance, Dover sole and Pacific sanddab, which were more abundant in deeper stations in this study, are found, as adults, at or beyond the shelf break. In contrast, species like English sole and butter sole, which were more abundant in shallow stations in this study, as adults, are found at or inshore of the shelf break (Allen & Pondella 2006).

Unfortunately, there is still a lack of information about species tolerance to hypoxic conditions at different stages of development. Since hypoxic conditions move from offshore to inshore with upwelling-driven currents (Grantham et al.

a.



b.

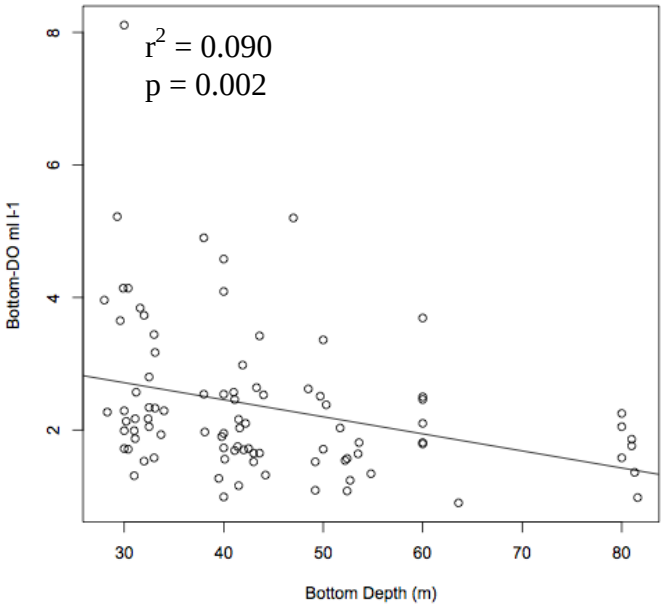


Figure 10. Correlation plot of a) bottom-DO (ml l^{-1}) and bottom-temperature (^{o}C) and b) bottom-DO (ml l^{-1}) and bottom depth (m) for all four study years.

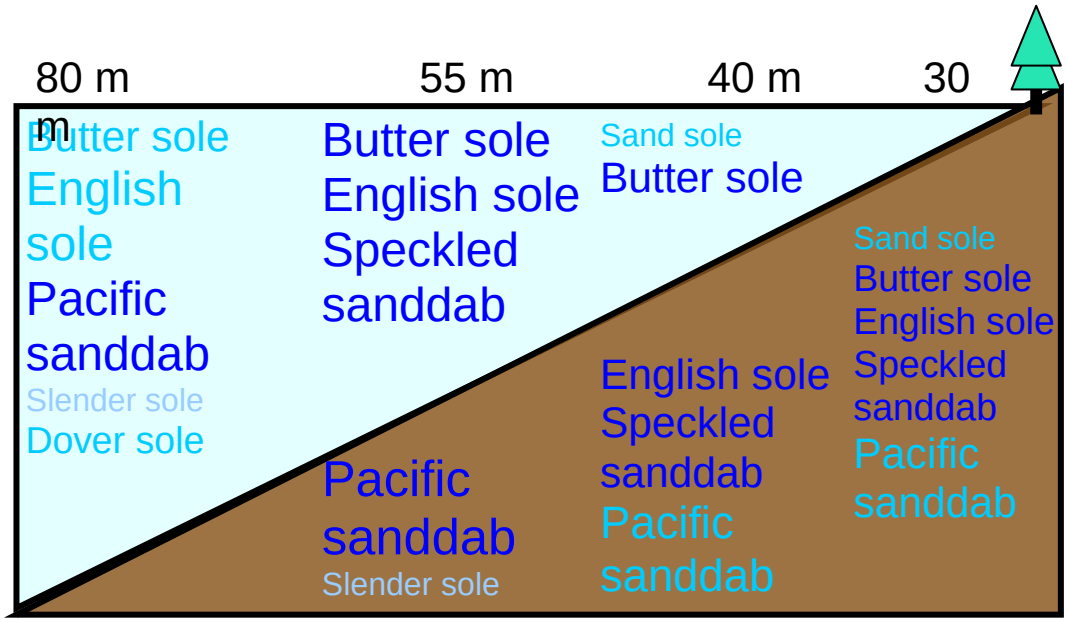


Figure 11. Changes in species abundance and species length with distance from shore, is indicated above. Color intensity denotes the change in species abundance in relation to distance from shore (the tree). The bolder blue color indicates a greater abundance. Font size denotes a change in species length in relation to distance from shore. Greater font size indicates larger fish.

2004, Chan et al. 2008), larger/older English sole, butter sole, and speckled sanddab are in contact with hypoxic conditions more frequently and for longer durations than smaller/younger fish. The more frequent exposure to hypoxic conditions by larger/older fish for English sole, butter sole and speckled sanddab would suggest that they most likely have a higher tolerance than smaller/younger fish. Therefore, unless the hypoxic zone reaches the shallower stations in which the smallest fish recruit, hypoxia may not have an adverse affect on the species.

Although Pacific sanddab were not found either as far inshore as English sole, butter sole, or speckled sanddab, nor caught at a small size (< 50 mm), it appears they are still using the nearshore waters around Moolack Beach (~ 80 m) as a habitat during their juvenile development stage. However, they appear to be recruiting (first settlement out of the water column) outside of this study's sampling area. Rooper et al. (2006) collected, Pacific sanddab ranging from 23 – 150 mm within four northwest estuaries (Willapa Bay, Grays Harbor, Coos Bay and Yaquina Bay). The size range Rooper et al. (2006) collected was much lower than the size range collected during this study in the nearshore settlement habitats (55 – 220 mm). One hypothesis would be that Pacific sanddab are recruiting to estuaries and then once larger, migrating to nearshore habitats. Therefore, in future studies, it may be prudent to sample both a nearshore coastal habitat and a nearby estuary (e.g., Moolack Beach and Yaquina Bay) in order to characterize the distributions of certain dominant species. A second hypothesis would suggest that Pacific sanddab are recruiting further offshore than my sampling area and

subsequently migrating into shallower waters. Extending the nearshore sampling into deeper water (> 80 m) would test the second hypothesis.

Previous studies have also shown a connection between estuaries and nearshore coastal nursery grounds for recruitment for juvenile English sole (Laroche & Holton 1979, Krygier & Pearcy 1986, Boehlert & Mundy 1987, Toole et al. 1987, Rooper et al. 2006). English sole have been shown to settle both in nearshore nursery grounds and estuaries (Krygier & Pearcy 1986, Boehlert & Mundy 1987, Toole et al. 1987). Some juvenile English sole that settle in the nearshore nursery grounds, however, appear to migrate into an estuary, where they may reside for a period of time before moving back to the nearshore nursery grounds (Krygier & Pearcy 1986, Boehlert & Mundy 1987). These migration patterns have been linked with tidal transport (Boehlert & Mundy 1987, 1988). The identification of the nearshore waters around Moolack Beach as suitable settlement habitat for English sole, butter sole and speckled sanddab, indicates a need for continued monitoring of species abundance and distribution when changes to the area such as the implementation of the wave energy test berths and the Yaquina dredge sediment dumping occur. Likewise, since estuaries are linked to the juvenile abundance of certain species within nearshore nursery grounds (Krygier & Pearcy 1986, Boehlert & Mundy 1987), more research focus should be devoted to monitoring the impacts of changes made to the estuary as well, such as future developments along the estuary coastline.

The nearshore waters (< 100 m) of central Oregon, particularly off Moolack Beach, are a highly diverse and complex ecosystem. Composed mostly of sandy bottoms and rocky outcroppings, they provide suitable settlement habitats for ecologically and commercially important species such as English sole, Dover sole, Pacific sanddab, and rockfishes, to name a few. With an expected increase in hypoxic conditions (Grantham et al. 2004, Chan et al. 2008) and increase need for spatial usage of coastal areas (Boehlert et al. 2007, Brekken et al. 2009) monitoring the successful settlement of the juveniles for the above species in this area during hypoxic conditions should continue.

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CHAPTER 4: CONCLUDING REMARKS

With this study, I begin to fill in the gaps of missing information about the effects of nearshore hypoxia on early life stages of fishes within the NCC. Most hypoxic studies on species within the United States have occurred on the East and Gulf coasts where anthropogenic inputs of nutrients cause annual hypoxic events. Along the NCC, hypoxia is not caused by anthropogenic inputs, but rather by wind forcing, upwelled-source water from the oxygen minimum zone (OMZ) and the respiration of an enriched nutrient load. However, with global climate change, the extent and intensity of hypoxic levels within the NCC could increase (Whitney et al. 2007). As the earth warms and sea level rises, wind patterns have started to change. Stronger and more intense wind forcing along the NCC during the summer could cause more intense and extensive upwelling, which in turn could cause expansive and temporarily extensive hypoxic events. Keeling et al. (2010) and Stramma et al. (2010) have already reported decreases in dissolved oxygen within the OMZ of the North Pacific and the tropical Pacific, Atlantic and Indian gyres due to global warming. Falkowski et al. (2011) also suggests that global warming could have an indirect effect on the extent and spatial distribution of nearshore hypoxic events within the NCC, since upwelled-driven source water comes from the OMZ.

As stated above, most studies looking at the effects of hypoxia have been focused on species within the Chesapeake Bay or northern Gulf Coast regions. Not until recently (the last 5-10 years or so), have the effects of hypoxia on fish species

within the NCC been examined and reported, and very few of those studies have looked at fish early life stages (Keller et al. 2010, Auth 2011). This project was able to examine the effects of hypoxia on fish species larval and juvenile abundance, composition, spatial distribution and body condition (juveniles only) in a possible nearshore nursery area. However, without knowing specific species responses (e.g. behavior and physiological) to DO, the impacts of hypoxia on the above metrics are not completely understood. For example, the abundance of juvenile English sole decreased with decreased bottom-DO, but this response could have been caused by factors other than bottom-DO. For example, both temperature and depth co-vary with dissolved oxygen, therefore either variable could have caused the response I found with English sole. Also, I am not able to say whether a lower abundance meant that English sole were dying or that they were swimming out of the sampled locations when bottom-DO began to decrease. Understanding the DO lethal and sublethal limits at the species level and which behaviors change as DO levels approach these limits would provide further insight into the results reported in this study.

Understanding species physiological responses to decreased DO levels is also important. Flatfish have been shown, in previous studies, to initiate energy-saving alternatives by reducing activity levels and depressing metabolism (Dalla Via et al. 1998). Prolonged exposure to hypoxia can cause fish to give preference to respiratory processes and disrupt hydromineral balance, and can cause long-term elevations in plasma cortisol. A disruption to hydromineral balance may

cause fish to decrease activity and enter into a state of metabolic depression. This depression may severely limit a response to other environmental factors such as predation, or in the case of my study, a limited response to our beam trawl. The fish could be more susceptible to capture, due to metabolic depression, causing my results to show an increase in species catch abundance with decreased bottom-DO when really the increase in catch abundance is due to a less responsive behavior of the fish as a result of decreased bottom-DO. Also, elevations in plasma cortisol can negatively impact growth, reproduction, and resistance to pathogens (Bonga 1997). Fish early life stages are relatively more vulnerable to low DO due to lower physiological tolerance, limited mobility, and increased lifetime exposure (Tallqvist et al. 1999, Vaquer-Sunyer & Duarte 2008). I found, however, that the body condition of newly recruited butter sole (< 75 mm) increased with decreased bottom-DO but I do not know what physiological changes, if any, were occurring within the fish to cause this type of response.

I was able to conclude that hypoxia does have an impact on species abundance, spatial distribution, and vertical distribution at early life stages within the NCC. The results of this study varied from species to species and with stage of development (e.g. recruiting, newly settled, settled juvenile, etc.). The NCC is home to many commercially important species and the Oregon and Washington coasts are home to settlement habitats for the juveniles of these species, which supply the adult populations fished along the coast. Understanding the impact of

hypoxia on the juveniles can therefore give an indication of the health and abundance of future adult populations and aid in managing these fisheries.

I suggest the following changes or additions to improve the success of this project. First, I suggest targeting smaller depth ranges near the seafloor with the MultiNet when investigating the effects of hypoxia on the vertical distribution of fish larvae. These shallower depth ranges will allow more sampling at the lower DO ranges. I would also suggest sampling with one net just below the hypoxic layer (< 2.0 ml l^{-1}), and a second net just above the hypoxic layer in order to investigate if larval fish are aggregating just above the hypoxic layer. Second, I suggest trying to implement a long-term DO monitoring system within nearshore (< 40 m) waters off of Moolack Beach. A near real-time data series would provide information on how long fish were exposed to hypoxic levels of bottom-DO. I compared the CTD bottom-DO measurements from my 30 m stations to measurements collected from a buoy roughly 24 miles north of the Newport Hydrographic line in 15 m of water to see if the bottom-DO values or trends matched (Fig. 12). I had hoped to compare the bottom-DO time-series data from the buoy to my species abundance data. However, the bottom-DO values did not match up indicating that these two regions, only ~ 24 miles apart, differ physically. Therefore, it is prudent to set up a long-term DO measurement station off of Moolack Beach to collect near real-time data, in order to successfully monitor the effects of hypoxia exposure on the species community. Finally, there still needs to be more understanding of individual species responses to low DO (e.g. lethal

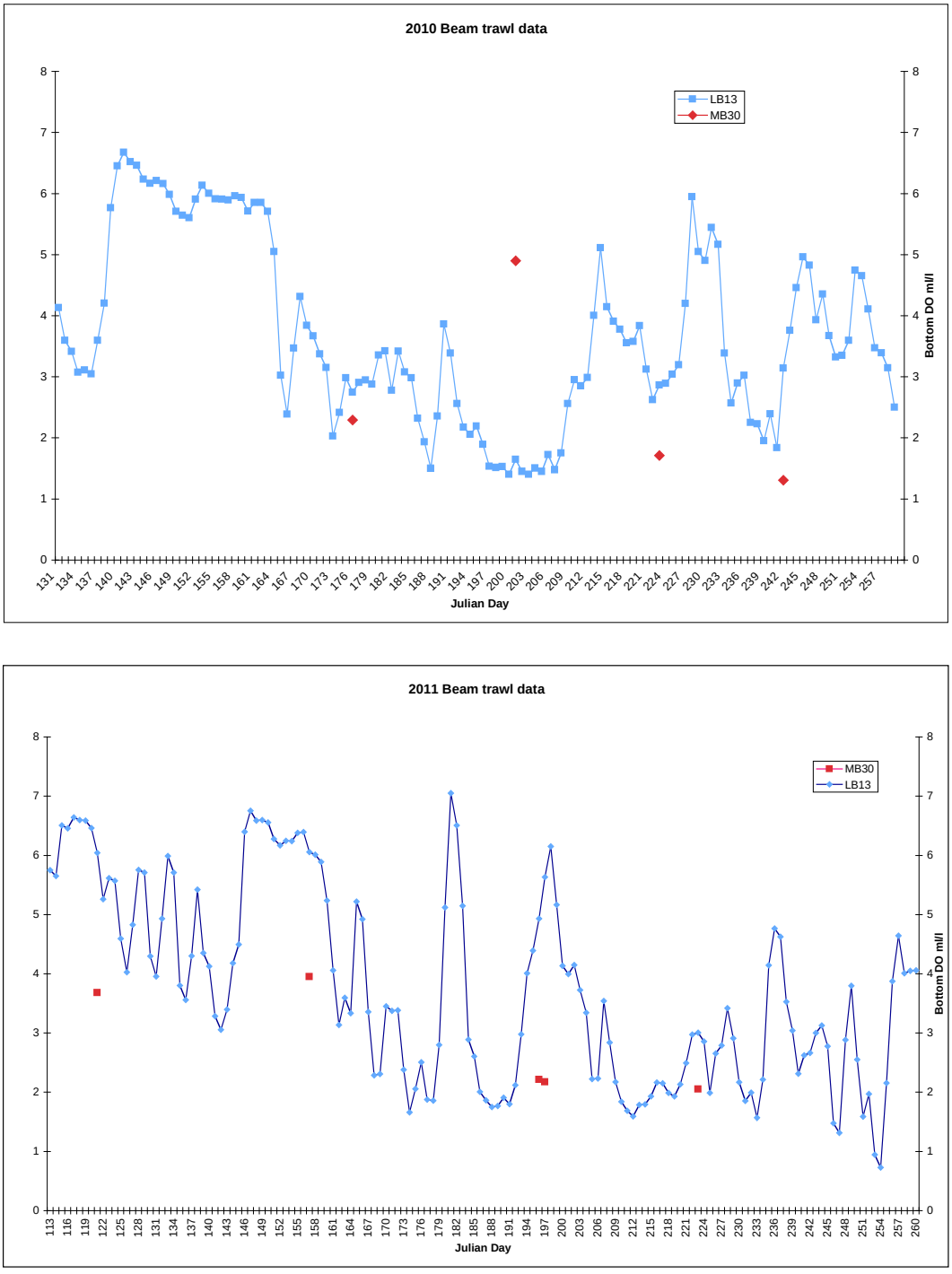

Figure 12. Daily average Bottom-DO values for the Lincoln Beach buoy (15 m) (blue dots & line) and daily average bottom-DO values for the 30 m stations in this study (red squares).

limits, behavioral changes, feeding habits, and physiological changes). I recommend investigating individual species responses to low DO in a controlled laboratory setting, in which species behavior and physiology can be observed and monitored on a continuous basis. These suggestions, if followed, should provide better insight into the effects of hypoxia on the nearshore larval and juvenile fish communities of the central Oregon and Washington coast.

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